

---

---

UNIVERSITY OF KANSAS PUBLICATIONS  
MUSEUM OF NATURAL HISTORY

---

Volume 18, No. 7, pp. 547-716, 110 figs., 12 pls.

---

April 13, 1970

---

Evolutionary Relationships  
of Casque-headed Tree Frogs  
with Co-ossified Skulls  
(Family Hylidae)

BY

LINDA TRUEB

UNIVERSITY OF KANSAS  
LAWRENCE  
1970

UNIVERSITY OF KANSAS PUBLICATIONS, MUSEUM OF NATURAL HISTORY

Editors: Frank B. Cross, Philip S. Humphrey, Robert M. Mengel

Volume 18, No. 7, pp. 547-716, 110 figs., 12 pls.

Published April 13, 1970

UNIVERSITY OF KANSAS  
Lawrence, Kansas

PRINTED BY  
ROBERT R. (BOB) SANDERS, STATE PRINTER  
TOPEKA, KANSAS  
1970



32-7038

# Evolutionary Relationships of Casque-headed Tree Frogs with Co-ossified Skulls (Family Hylidae)

BY

LINDA TRUEB

## CONTENTS

	PAGE
INTRODUCTION .....	551
Acknowledgments .....	552
Materials and Methods .....	552
Cranial Anatomy of a Generalized Hylid Frog .....	554
CRANIAL OSTEOLOGY OF <i>Tripriorion petasatus</i> .....	558
External Dermal Bones of the Olfactory Region .....	558
Internal Bones and Cartilages of the Olfactory Region .....	560
The Sphenethmoid and External Dermal Bones Associated with the Sphenethmoid .....	569
Internal Bones and Cartilages of the Sphenethmoid Region ..	571
External Bones of the Orbital, Otic, and Occipital Regions ..	574
Internal Bones and Cartilages of the Orbital, Otic, and Occipital Regions .....	574
The Bursa Angularis Oris .....	580
The Articular Region .....	580
Summary of the Description of the Skull of <i>Tripriorion petasatus</i> .....	580
COMPARISON OF THE CRANIAL MORPHOLOGY OF <i>Tripriorion</i> <i>petasatus</i> AND <i>Smilisca baudini</i> .....	582
The Olfactory Region .....	584
The Sphenethmoid and Orbital Region .....	585
The Otic and Occipital Regions .....	585
The Bursa Angularis Oris .....	586
The Articular Region .....	586
Discussion .....	586
DEVELOPMENT OF THE OSTEOCRANIUM OF <i>Tripriorion petasatus</i> ..	588
The Membrane Bones .....	588
The Cartilage Bones .....	593
COMPARATIVE DEVELOPMENT OF THE OSTEOCRANIUM .....	594

	PAGE
THE OCCURRENCE OF THE CASQUE-HEADED, CO-OSSIFIED CRANIUM	
WITHIN THE HYLIDAE	598
Synopsis of the Genera	599
Cranial Morphology of <i>Hyla septentrionalis</i>	603
Cranial Morphology of <i>Osteocephalus taurinus</i>	612
Cranial Morphology of <i>Trachycephalus nigromaculatus</i>	620
Cranial Morphology of <i>Trachycephalus jordani</i>	629
Cranial Morphology of <i>Corythomantis greeningi</i>	633
Cranial Morphology of <i>Aparasphenodon bruno</i>	642
Cranial Morphology of <i>Pternohyla</i>	651
Cranial Morphology of <i>Triprior spatulatus</i>	664
VARIATION IN CRANIAL ELEMENTS IN CASQUE-HEADED,	
CO-OSSIFIED HYLIDS	673
The Olfactory Region (including the upper jaw)	674
External Dermal Bones	674
Internal Bones and Cartilages and Associated Structures	677
Relationship of Internal to External Structure	680
The Sphenethmoid and Associated Bones	681
The Orbital, Otic, and Occipital Regions	683
External Dermal Bones	683
Internal Bones and Cartilages	685
Bursa Angularis Oris	686
The Articular Region	686
EVOLUTIONARY RELATIONSHIPS OF THE CASQUE-HEADED,	
CO-OSSIFIED HYLIDS	687
The <i>Hyla septentrionalis</i> Group	688
<i>Aparasphenodon</i> and <i>Corythomantis</i>	689
<i>Osteocephalus</i> and <i>Trachycephalus</i>	692
<i>Triprior</i> and <i>Pternohyla</i>	696
CONCLUSIONS	698
SPECIMENS EXAMINED	704
GLOSSARY	706
LITERATURE CITED	713

## INTRODUCTION

In comparison with the more plastic external features, the skeletal elements of vertebrates are generally considered to be evolutionarily conservative. Because of the relative stability of skeletal features, these characters have been relied upon heavily in the classification of higher categories and in the determination of general evolutionary trends. External morphological variation in color, general form, and particular structure is well known in hylids. Internal morphology, on the other hand, has been largely ignored in favor of the more readily apparent external characters. Our knowledge of the osteology of hylids is particularly deficient.

There seems to be remarkably little variation in the postcranial skeleton in hylids. Cranially, hylids are generally marked by a trend towards reduced ossification compared with frogs of most other families. However, within the hylids there are several genera which seem to represent a contradiction to the evolutionary trend of the rest of the group. These are the so-called "helmeted" hylids having heavily ossified skulls molded into solidly roofed and extraordinarily bizarre cranial formations of crests, ridges, and flanges. The unusual condition of the skulls in these genera has led to their widespread designation as the "casque-headed hylids."

These peculiar frogs were first brought to my attention by the acquisition of a large series of adults and a developmental series of young *Triprion petasatus*, one of the strangest of the casque-headed hylids. Originally, it was my intention to trace the development of the cranium in this species in an attempt to understand how the adult acquired such an unusual skull. The next logical step in the investigation was a comparison of the developmental and adult cranial morphology of *Triprion* with a presumably generalized hylid. The study was carried to its logical conclusion by an investigation of the other genera of casque-headed hylids. Several authors (Carvalho, 1941; Myers, 1942; Peters, 1955; Smith, 1957; and Rivero, 1961) have commented on the phylogenetic relationships of the casque-headed hylids. On the whole their work was based on superficial examination; the authors were hindered by insufficient knowledge of the basic structures of the skulls and the derivations of the cranial modifications.

My investigations of the cranial osteology of these frogs and a wide array of other hylids have led to the formulation of a phylogenetic arrangement which seems to show that the casque-headed

hylids have been derived from several phyletic lines. In each case the individual lines have undergone similar types of modifications in response to similar environmental situations. These frogs, which seemingly represent a reversal in the evolutionary trend in hylids, show several unique morphological characteristics by which they are functionally adapted to specialized modes of existence, first alluded to by Cope (1865:194) in reference to *Triprion petasatus*: "It is interesting that an animal living in rocky situations should present such a cranial bony development; this, in connection with its colors, no doubt, aids especially in concealment, and is another instance of the Creator's bountiful care for his humblest creatures."

### Acknowledgments

The completion of this study has been possible largely through the cooperation of museum curators and owners of private collections who have loaned, donated, or provided data for many valuable specimens. For their cooperation, I thank Mr. Werner C. A. Bokermann and Drs. Konrad Klemmer, Robert F. Inger, Alan E. Leviton, Richard B. Loomis, James A. Peters, Edward H. Taylor, and Charles F. Walker. I am indebted to the numerous persons who have offered their time, suggestions, and critical advice during the course of my work. Dr. Richard J. Baldauf provided valuable assistance in the correct preparation and interpretation of serial cross-sections during the initial stages of this study. Mr. John Lynch proffered countless ideas, many of which were instrumental in the formulation of my own thought. I am grateful to Dr. Theodore H. Eaton and Dr. Gerald R. Smith for their generous and time-consuming cooperation in providing thorough and critical evaluations of this manuscript. I thank Dr. Smith especially for preparing several stereo radiographs of rare species, which otherwise could not have been included in this study. The greatest single debt of gratitude is to Dr. William E. Duellman, who, by his encouragement and aid is responsible for the initiation, development, and realization of this study in its present form. Particular thanks are extended to Miss Martha Crump who spent many long and tedious weeks in the preparation of much of the skeletal material and many of the thousands of serial cross-sections of frog heads used in this work. I am indebted to Mrs. Donna L. Ford for her willing and competent secretarial assistance in the transcription of this manuscript to its final form. For his assistance in field work in México, I thank Mr. Erwin E. Klaas. The study was supported by grants (GB-1441 and GB-5818) from the National Science Foundation, William E. Duellman principal investigator.

### Materials and Methods

The descriptive accounts and discussions which follow are based on the study of 374 osteological preparations (254 dried skeletons, 99 cleared and stained specimens, and 21 sets of serial cross-sections; see list of specimens examined). Radiographs were made of four other specimens; three of these were stereo radiographs prepared by the method described by Smith and Smith (1967).

Dried skeletons were prepared from preserved specimens or by means of dermestid beetles from carcasses dried in the field. Cleared and stained preparations were obtained from specimens stored either in 70 per cent alcohol or 10 per cent formalin. Specimens were cleared in two per cent potassium hy-

dioxide, and the ossified parts of the skeletons were stained with alizarin sulfonate of sodium; final preparations were stored in glycerin.

Most specimens used for sectioning were fixed and preserved in 10 per cent formalin. One dried skull was used, somewhat unsuccessfully, in the preparation of serial cross-sections. The entire heads were sectioned exclusive of the lower jaw anterior to the articular region. Sections were cut between thicknesses of 10 and  $35\mu$ , depending upon the size of the specimen and the area of the cranium being sectioned. It was found that large skulls could be sectioned at thicknesses ranging between 25 and  $35\mu$  without suffering distortion or loss of visible detail of internal structure, whereas small skulls were more satisfactorily sectioned between thickness of 10 and  $20\mu$ . Sections made through the olfactory regions of the crania were cut 5 to  $10\mu$  thinner than sections made through posterior parts of the skull.

Baldauf's (1958b) suggested procedures for the preparation, staining and sectioning of adult anuran heads were followed. A few modifications of his technique are worth noting. For most anurans three days are minimally necessary for decalcification in Perényi's Fluid; five to six and one-half days are required for large anurans or frogs with heavily ossified or co-ossified skulls. No tissue damage has been observed in smaller specimens which have been in Perényi's Fluid as long as six and one-half days. I suggest that Baldauf's staining schedule be modified for larger material, cut at thicknesses between 20 and  $25\mu$ , to include two initial changes of xylol at a maximum time of five minutes each. Azocarmine G must be substituted for Azocarmine B, a biological stain which apparently is no longer available. Only 11 to 15 minutes are required to stain sections cut at  $20\mu$  in Azocarmine G, compared to the 30 minutes indicated for Azocarmine B in Baldauf's Heidenhain's Azan technique.

The following descriptive accounts are organized in the same manner. The skull has been divided arbitrarily into the following sections: olfactory region (including the upper jaw); sphenethmoid and orbital regions; otic and occipital regions; and the articular region. At the beginning of each account a diagnostic list of morphological characters is provided for the species. Within each succeeding section, external dermal bones are discussed first and followed by internal bones and cartilage. The first descriptive account, that of *Triprrion petasatus*, is the most detailed. The successive accounts are more general and do not deal with characters that do not show significant variation. Unless specifically stated otherwise, all descriptions are given in an anterior to posterior sequence.

Repeated use has been made of such terms as "appears," "extends," and "level." The reader should view the meaning of these terms in the context of the study at hand. Thus "level" is any transverse plane, perpendicular to a line lying between the anterior and posterior ends of the skull. With respect to sets of serial cross-sections used, each cross-section represents a different level of the skull. Words such as "appears" and "extends" should be interpreted in the dynamic sense, so that as we progress through the skull, level by level, by means of serial cross-sections, various structures "extend" from one level to another, or "appear" at a certain level. Particular care should be exercised not to give words such as "appearance" the chronological connotation common in developmental studies. An effort has been made to provide reasonable and consistent anatomical designations. These are based on studies of Baldauf (1955; 1957; and 1958a) and Baldauf and Tanzer (1965); changes in termi-

nology involve the anglicization of Latin terms which are commonly used in English and awkward to use in Latin. A glossary of terms used, their derivation, and definitions follows the list of specimens examined.

All illustrations of cross-sections were made by use of a microprojector. Only bone, cartilage, and the external outline of the head are shown. Each account (except *Trachycephalus jordani*) is illustrated by two or three cross-sections of the anterior end of the skull and followed by illustrations at the levels of all of the cranial nerve foramina except the trochlear foramen, and the jugular foramen of *Corythomantis greeningi*. Dorsal and ventral views of the skulls of a member of each genus or species group are provided.

### Cranial Anatomy of a Generalized Hyloid Frog

The data and conclusions which follow are based on the premise that a thorough understanding of the structure of the anuran skull is obtained by examination of both external and internal features. Unfortunately, external similarities between the skulls of two species often mask internal differences, or, in some instances, the converse may be true. Internal anatomy principally involves the structure of the chondocranium and/or endochondral bones derived from the chondocranium. I think the endochondral cranial structure among hylids has been subject to much less evolutionary and adaptive alteration than have bones of dermal origin; therefore, variation involving internal structures should be carefully evaluated. Examination of internal anatomy is possible through use of serial cross-sections. Interpretation of serial sections is often difficult for the casual reader. I have prepared below a description of the anatomy of a generalized hylid skull. The account is functionally oriented, relating internal to external anatomy, in order to make the descriptions which follow more easily understood.

Functionally, the structure of the hylid skull fulfills at least three important needs. The braincase is a receptacle for sense organs (the eyes, ears, and nose), and it houses the central nervous system; the jaws provide a mechanical system for the ingestion of food. Several dermal bones suspend, or brace the jaws against the central braincase, and dermal covering bones form a protective casing around the braincase and sense organs.

The nasal capsules are the most anterior sense organs of the cranium. The capsules lie between the maxillaries and posterior to the premaxillaries; they form an anterior extension of the sphenethmoid. Dorsally the olfactory region is covered by the nasals and anteroventrally it is protected by the prevomers (Fig. 1). A nasal capsule consists of three cavities lying above one another. The nasal cavities are encased in cartilage and supported internally by carti-

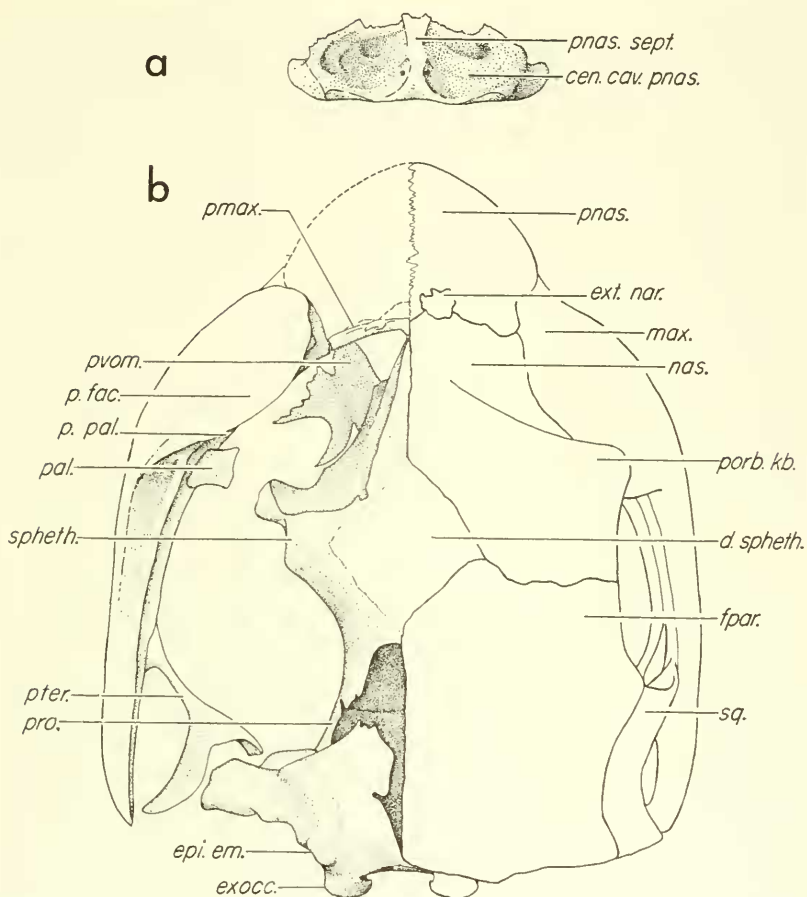


FIG. 1. Partially disarticulated skull of *Triprion petasatus* (KU 71759), ♂.  $\times 4$ : (a) posterior view of prenasal; (b) dorsal view of skull with left frontoparietal, squamosal, quadratojugal and nasal, left half of prenasal removed. Abbreviations: *cen. cav. pnas.*, central cavity of prenasal; *d. spheth.*, dermal sphenethmoid; *epi. em.*, epiotic eminence; *exocc.*, exoccipital; *ext. nar.*, external naris; *fpar.*, frontoparietal; *max.*, maxillary; *nas.*, nasal; *p. fac.*, pars facialis of maxillary; *p. pal.*, pars palatina; *pal.*, palatine; *pmax.*, premaxillary; *pnas.*, prenasal; *pnas. sept.*, prenasal septum; *porb. kb.*, preorbital knob; *pro.*, prootic; *pter.*, pterygoid; *pvom.*, prevomer; *spheth.*, sphenethmoid; *sq.*, squamosal.

lage and bone (the prevomer and septomaxillary). The cavum principale is the largest and dorsalmost of the nasal cavities; the external naris opens into the anterior end of this cavity. The cavum medium is a small cavity which lies beneath the anterior end of the cavum principale. Structurally the cavum medium is important because its posterior bifurcation produces the nasolacrimal duct laterally; medial to the nasolacrimal duct, the cavum principale

opens from above and the *cavum inferius* from below into the *cavum medium*. The *cavum inferius* is a large, depressed cavity which lies ventral to the *cava principale* and *medium*. At the posterior terminus of the *cavum medium*, the *cava principale* and *inferius* unite via the *cavum medium*, and extend posteriorly as a single, large cavity into which the olfactory eminence protrudes ventrally and the internal naris opens posteriorly.

Anteriorly two rods of cartilage, the superior and inferior prenasal cartilages, extend from the premaxillary to the nasal capsule posteriorly. The superior prenasal cartilage fuses with the alary cartilage which surrounds the anterolateral part of the *cavum principale* posterior to the opening of the external nares. The inferior prenasal cartilage fuses with the cartilaginous floor of the nasal capsule, the *solum nasi*, anteromedial to the prevomer. The anterior part of the olfactory capsule is formed of four parts, the alary cartilage laterally, the *solum nasi* ventrally, the *septum nasi* medially, and the *tectum nasi* dorsally. The *cava medium* and *inferius* lie ventral to the *cavum principale* and protrude anteriorly into the *solum nasi*, dividing the latter into three layers. The ventral layer of cartilage, lying between the prevomer and the *cavum inferius* is the *solum nasi*. The cartilage separating the *cavum inferius* and *cavum medium* is the *lamina inferior* and that separating the *cavum medium* and *cavum principale*, the *lamina superior*. The septomaxillary bone lies in the *lamina superior* and supports the confluence of the *cavum principale* and *cavum medium* and the divergence of the nasolacrimal duct from the *cavum medium*.

Between the levels of the external and internal nares, lateral support of the nasal capsule is furnished by the *planum terminale*, which forms by the fusion of the *cartilago obliquo* (which diverges dorsolaterally from the *tectum nasi*) and the posterolateral end of the *lamina inferior* lateral to the *cavum principale*. The *solum nasi* and *septum nasi* provide ventral and medial support, respectively, of the nasal capsule at the level of the internal nares. At the posterior margin of the internal naris, the *solum nasi* fuses with the *planum antorbitale* laterally to encase the nasal capsule completely. Ventrally, the *solum* is underlain by the palatine; dorsally and laterally, the nasal capsule is covered by the nasal bone. The cartilage surrounding the posterior ends of the nasal cavities is replaced by the bones of the sphenethmoid.

The orbits are formed by several bones and cartilages. The *planum antorbitale* and the overlying nasal bone form the anterior

margin of the orbit, the maxillary the ventral margin, and the anterior arm of the squamosal the posterior margin. The medial aspect of the orbit is formed by the cartilaginous sclera surrounding the internal and proximal surface of the eye, which lies adjacent to the braincase.

The otic region is encased by the prootic. The otic capsule lies posterior to the orbit and lateral to the braincase; the capsule is formed by the ventrolateral part of the prootic. The dorsolateral part of the prootic, the crista parotica (Fig. 1), forms the roof of the otic capsule and extends laterally to articulate with the anterior and posterior arms of the squamosal. The columella, or stapes, lies ventral to the crista parotica and consists of three parts. The distal end of the columella, the pars externa plectri, is cartilaginous and lies adjacent to the tympanic membrane. The pars externa plectri is suspended from the distal end of the crista parotica by a small rod of cartilage, the pars ascendens plectri. Proximally, the pars externa plectri attaches to the bony medial part of the columella, the pars media plectri. The proximal end of the columella is formed by the cartilaginous pars interna plectri which lies between the pars medial plectri and the otic capsule and articulates with the cartilaginous operculum posteriorly. The operculum lies over the foramen ovale in the posterolateral part of the otic capsule.

The braincase is formed by three endochondral bones and two dermal investing bones. The sphenethmoid (Fig. 1) surrounds the anterior end of the brain. The bone lies between the olfactory capsule anteriorly and the prootic posteriorly, and is in synchondrotic continuity with both structures. The posterior part of the brain is housed by the prootic and exoccipital which are synosteotically united in adult frogs. Ventrally, the cartilaginous union of the sphenethmoid and prootic and the venter of the otic capsule are supported by a dermal investing bone, the parasphenoid. Dorsally, the frontoparietal overlies the posterior part of the sphenethmoid and the tectum synoticum of the prootic, forming a partial or complete bony roof to the braincase.

The upper jaw of a hyliid is composed of paired premaxillaries anteriorly, maxillaries laterally, and quadratojugals posterolaterally. The premaxillaries bear slender dorsal processes, the alary processes, against which the superior and inferior prenasal cartilages of the olfactory capsule abut. Posteriorly the maxillaries overlap the quadratojugal laterally. Near the posterior end of the quadratojugal, the ossification of the latter invades the cartilage of the

quadrate process which lies medial to the quadratojugal. The quadrate process articulates with the ventral arm of the squamosal dorsally, the posterior ramus of the pterygoid medially and Meckel's cartilage ventrally. Together, all these elements compose the articular region of the jaw. The lower jaw is composed of the paired endochondral mentomeckelian bones anteriorly, dermal dentary bones which laterally invest Meckel's cartilage, and posterolaterally, the dermal angulosplenials lying ventrolateral to Meckel's cartilages.

The principal function of the palatine and pterygoid is to brace the upper jaw against the braincase. The palatine articulates with the maxillary and sphenethmoid and forms the posterior margin of the internal nares. The pterygoid consists of three rami. The anterior ramus lies medially adjacent to the maxillary and cartilaginous posterior maxillary process in the region of the orbit. The medial ramus extends toward and sometimes articulates with the antero-ventral corner of the otic capsule. The third, posterior ramus of the pterygoid articulates with the medial surface of the quadrate process posteriorly.

### CRANIAL OSTEOLOGY OF *Tripriion petasatus*

The skull of *Tripriion petasatus* is longer than wide (Pl. 2a and b; Fig. 1). All dorsal surfaces of the skull are involved in integumentary-cranial co-ossification. Dorsally, all dermal bones are finely sculptured in a pattern of parallel or reticulate ridges. The distal margins of all dermal bones terminate in small spinose protuberances; the latter are best developed on the outer edges of the maxillary and the prenasal, the canthal ridge near the orbit, and the occipital crest. The skull of *Tripriion petasatus* is characterized by the presence of a dermal sphenethmoid, a prenasal, and extensive labial flanges on the maxillary and prenasal anterior to the orbit. The vocal sac is bilobed and subgular.

### EXTERNAL DERMAL BONES OF THE OLFACTORY REGION

The dermal bones of the olfactory region include the prenasal (*pnas.*), premaxillary (*pmax.*), septomaxillary (*spmax.*), prevomer (*pvom.*), palatine (*pal.*), and the anterior parts of the maxillary (*max.*) and nasal (*nas.*).

*Prenasal.*—The prenasal, named here for its external association with the nasals and external nares, lies anterior to the premaxillaries and nasals (Pls. 2a, b and 3a; Fig. 1a, b). The bone is approximately triangular in dorsal, ventral, and cross-sectional views (Figs. 1-4); the dorsal surface is involved with integumentary-cranial co-ossification. The posterior margin of the prenasal is connected by bony sutures to the maxillaries distally, and to the nasals dorsomedially, except where the prenasal forms the anterior margin of the external nares. Ventromedially, the posterior margin of the prenasal lies adjacent to the premaxillaries; it is separated from the latter by dense connective tissue.

*Premaxillary.*—Because of the presence of the prenasal anteriorly, the premaxillary is largely internal; only the pars dentalis of the premaxillary, lying

along the posteroventral margin of the prenasal, is visible in ventral view (Pl. 2b). The premaxillaries are narrowly separated medially by connective tissue; laterally the bone is separated from the pars palatina (*p. pal.*) and the pars dentalis of the maxillary by an area of dense connective tissue. A small, but well-developed palatine process is present posteromedially on the premaxillary. The palatine processes are separated from each other by a thin area of dense connective tissue. The premaxillary bears a large alary process about 4.5 times as long as the pars dentalis of the premaxillary is deep. The alary process is strongly convex and anterodorsally lies within cavities in the prenasal bone.

*Prevomer.*—In ventral view (Pl. 2b; Fig. 1b), the prevomer lies lateral to the midline of the skull and ventral to the solum nasi and the sphenethmoid. The anterior end of the prevomer lies dorsal to the lateral part of the pars palatina of the premaxillary; the posterior, dentigerous part of the bone lies at a slight angle and just lateral to the midline. Laterally the prevomer bears a delicate, wing-like extension which forms the anterior and anteromedial margins of the internal nares. The prevomerine dentigerous processes are small and transverse. Internally, the anterior end of the prevomer lies dorsal to the premaxillary and is associated with the ventral surface of the solum nasi at the level of the infundibulum (Fig. 9). Posteriorly, the prevomer expands dorsally to provide a bony support of the olfactory eminence (*olf. em.*, Figs. 12-13).

*Palatine.*—The palatine (Pl. 2b; Fig. 1b) is a flat, rectangular-shaped bone which lies lateral to the internal nares. The distal end is lodged in connective tissue between the pars facialis and pars palatina of the maxillary (Figs. 14 and 15). The palatine extends dorsomedially from the maxillary; the proximal end lies ventral to the lateral wall of the nasal. The bone is edentate.

*Nasal.*—The nasal is extremely large (Pls. 2a and 3a; Fig. 1b). Anteriorly the nasal articulates with the prenasal except where the nasal forms the posterior margin of the external nares. Laterally the nasal is attached to the pars facialis (Pl. 3a) of the maxillary, and posterolaterally, it forms the bony anterior margin of the orbit. Medially and anterior to the dermal sphenethmoid (*d. spheth.*, Pl. 2a; Fig. 1b) the nasals converge. The posterior margin of the nasal is attached by a bony suture medially to the anterior margin of the dermal sphenethmoid and laterally to the anterior margin of the frontoparietal (*fpar.*). The dorsal surface is completely involved in integumentary-cranial co-ossification. The nasal bears a well developed canthal ridge extending from the anterior medial margin to terminate in a large, spiny preorbital knob at the anterodorsal corner of the orbit (Pls. 2a and 3a; Fig. 1b). Lateral to the canthal ridge the surface of the nasal is striated; the striations parallel the canthal ridge. Medial to the canthal ridge, the striations form a radiate pattern centered about three-fourths of the distance from the anterior to the posterior end of the nasal and midway between the supraorbital margin of the nasal and the edge of the dermal sphenethmoid.

*Maxillary.*—The maxillary is large, massive, and deeply concave dorsally; throughout most of its length the maxillary bears a broad flange extending dorsolaterally from the pars dentalis of the bone (Pls. 2b and 3a). The flange is most extensive anterior to the orbit, reduced in width lateral to the orbit, and moderately developed posterior to the orbit. The dorsal surface of the maxillary is involved in integumentary-cranial co-ossification. Medially, the maxillary bears a well developed pars palatina (Pl. 2b; Fig. 1b) extending the length of

the bone dorsal to the pars dentalis. The process is most pronounced in the dentigerous region. Dorsal to the pars palatina and anterior to the orbit, the maxillary bears a large pars facialis (Fig. 1b). It is this part of the maxillary that lies adjacent to the nasal and posteriorly forms the bony ventral margin to the anterior edge of the orbit. Posteriorly, the quadratojugal (*qj.*) lies within a slight medial depression of the maxillary formed by the extension of the pars palatina from the dentigerous region (Pl. 2b).

### INTERNAL BONES AND CARTILAGES OF THE OLFACTORY REGION

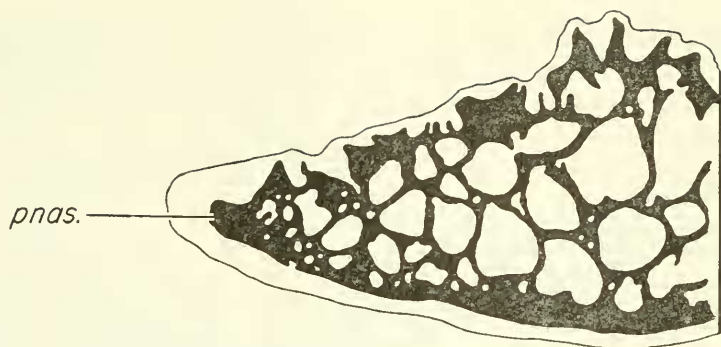
*Prenasal and Alary Process of Premaxillary.*—Internally, the anterior part of the prenasal (Fig. 2) is characterized by a thick ventral base overlain by a series of small cavities. Farther posteriorly, the central cavities coalesce to form a large cavity (Fig. 3). The cavity is filled with fat and blood vessels and is flanked on either side by two to four smaller cavities. At about one-half the length of the prenasal, the central cavity is separated by a bony vertical septum called the prenasal septum (*pnas. sept.*). The alary process (*al. proc.*) of the premaxillary lies within the two larger cavities separated by the prenasal septum (Fig. 4). The prenasal persists dorsomedially to a level just posterior to the external nares where it is replaced by the nasals (Figs. 5 and 6).

*Alary cartilage.*—The alary cartilage (*al. c.*, Figs. 4-5 and 7a, b) appears slightly posterior to the superior prenasal cartilage. The anterior end of the alary cartilage lies within the prenasal cavity just posterior to the tip of the alary process of the premaxillary. In subsequent sections the cartilage becomes arcuate in shape and lies along the lateral edge of the prenasal cavity. Immediately anterior to the external nares the alary cartilage joins the tectum nasi (*tect. nas.*) dorsally to form a roof over the anterior end of the cavum principale (*cav. prin.*). The cartilage diminishes in size and disappears shortly posterior to the appearance of the cavum medium (*cav. med.*).

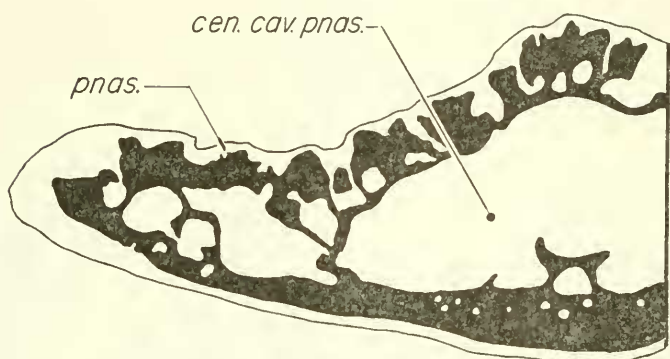
*Tectum nasi.*—The tectum nasi (Fig. 4) is present only in anterior sections between the anterior end of the alary cartilage and the posterior end of the prenasal septum. The unusually short tectum nasi lies just medial to the central part of the prenasal. The tectum meets the alary cartilage dorsal to the cavum principale, and expands ventromedially to join the anterior end of the septum nasi (*sept. nas.*). In sections posterior to the opening of the external nares (Fig. 5) the tectum is reduced to a small dorsal flange-like projection of the septum nasi which supports the edge of the nostril lateral to the medial part of the prenasal. Just anterior to the posterior edge of the nostril the tectum nasi terminates. At this point the cartilago obliqua (*c. obl.*, Fig. 6) diverges dorso-laterally from the septum nasi.

*Prenasal cartilages.*—The anterior end of the superior prenasal cartilage lies against the posterodorsal surface of the alary process of the premaxillary. The cartilage joins the alary cartilage posteriorly. The inferior prenasal cartilage (*inf. pnas. c.*) appears on the posteromedial surface of the base of the alary process of the premaxillary (Fig. 6) at a level of the anterior end of the recessus medialis (*rec. med.*) of the cavum inferius. The cartilage extends dorsally (Fig. 8) and fuses with the solum nasi (*sol. nas.*) at the posterior levels of the septomaxillary where the cavum principale is confluent with the cavum inferius (*cav. inf.*).

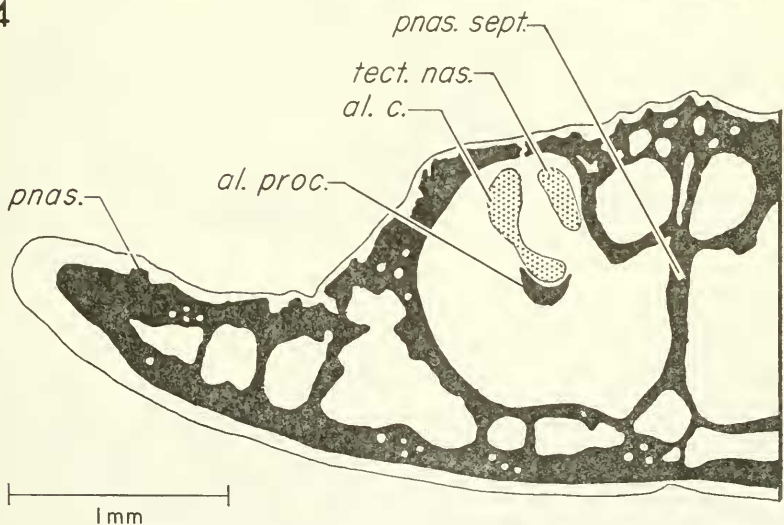
2



3

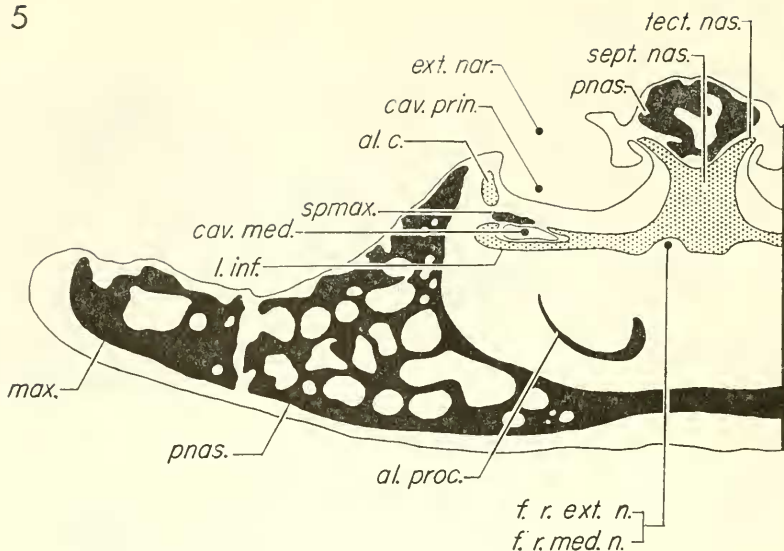


4

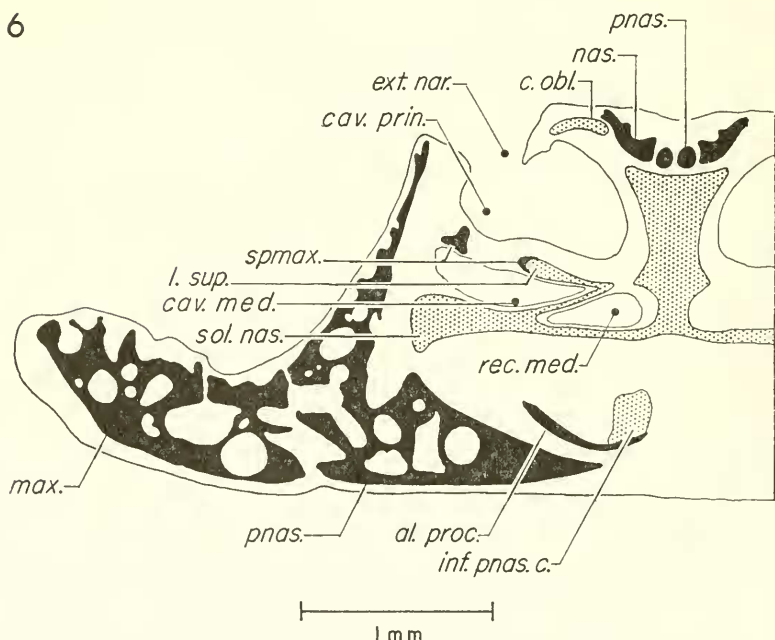


FIGS. 2-4. Transverse sections through prenasal at anterior end of skull of *Tripurion petasatus* (KU 71745): (2) anterior end of prenasal; (3) central cavity of prenasal; (4) prenasal septum. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *cen. cav. pnas.*, central cavity of prenasal; *pnas.*, prenasal; *pnas. sept.*, prenasal septum; *tect. nas.*, tectum nasi.

5



6



FIGS. 5-6. Transverse sections through anterior end of olfactory capsule of *Triprior petasatus* (KU 71745): (5) anterior level of cavum medium; (6) level of recessus medialis of cavum inferior. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *c. obl.*, cartilago obliquus; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *ext. nar.*, external naris; *f. r. ext. n.*, foramen ramus externus narium; *f. r. med. n.*, foramen ramus medialis narium; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *pnas.*, prenasal; *rec. med.*, recessus medialis of cavum inferior; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary; *tect. nas.*, tectum nasi.

*Septum nasi.*—The septum nasi (*sept. nas.*) replaces the prenasal septum posteriorly. The anterior end is connective tissue which unites the tecta nasi medially at a level anterior to the cavum principale. Cartilage (other than the tecta nasi) is first associated with the septum in the lateral part of the solum

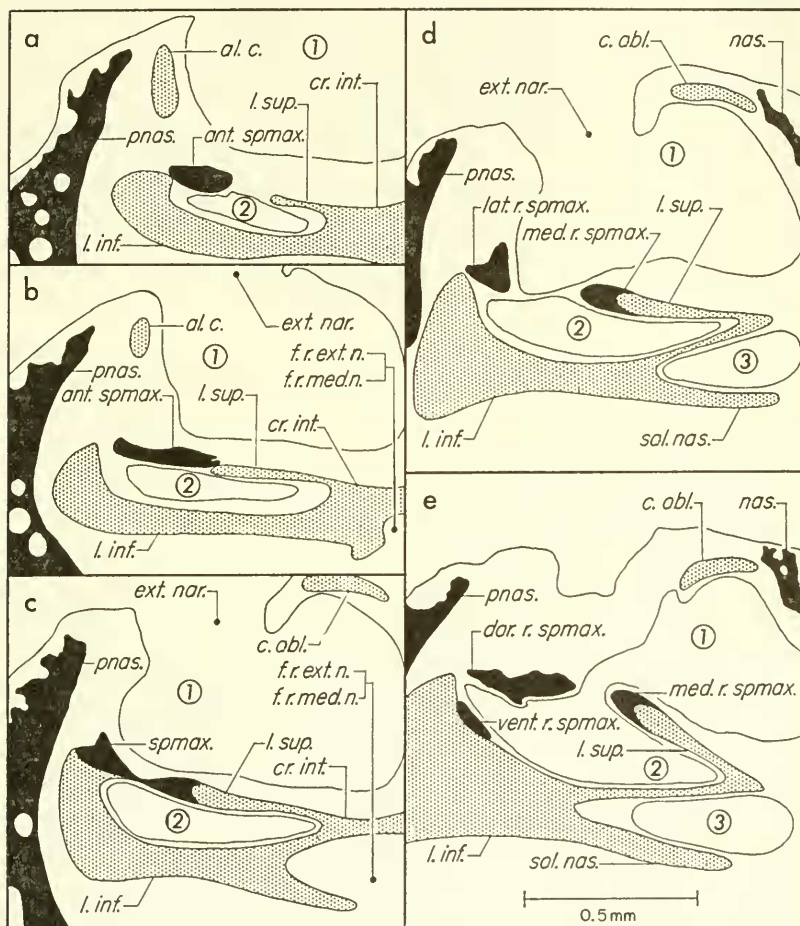


FIG. 7. Transverse sections through olfactory capsule of *Triprion petasatus* (KU 71745) in region of septomaxillary: (a-b) anterior end of septomaxillary; (c-d) medial divergence of septomaxillary; (e) dorsal, ventral, and medial rami of septomaxillary. Encircled numbers represent the nasal cavities as follows: 1) cavum principale; 2) cavum medium; and 3) recessus medialis of cavum inferius. Abbreviations: *al. c.*, alary cartilage; *ant. spmax.*, anterior end of septomaxillary; *c. obl.*, cartilago obliquus; *cr. int.*, crista intermedia; *dor. r. spmax.*, dorsal ramus of septomaxillary; *ext. nar.*, external naris; *f. r. ext. n.*, foramen ramus externus narium; *f. r. med. n.*, foramen ramus medialis narium; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *lat. r. spmax.*, lateral ramus of septomaxillary; *med. r. spmax.*, medial ramus of septomaxillary; *nas.*, nasal; *p.nas.*, prenasal; *sol. nas.*, solum nasi; *spmax.*, septomaxillary; *vent. r. spmax.*, ventral ramus of septomaxillary.

nasi at the level of the anterior ends of the septomaxillary and cavum medium. In subsequent sections, the connective tissue is replaced in distal areas first, until the septum nasi is completely cartilaginous at the level of the foramen ramus externus narius (*r. ext. n.*) and ramus medius narius (*r. med. n.*, Fig. 5). Peripheral ossification appears first at the level just anterior to the posterior end of the recessus medialis followed posteriorly by internal ossification (Fig. 11). The dorsal part of the septum nasi is the last to ossify. At the level of the olfactory eminence (Fig. 12) the septum nasi is completely ossified. Posteriorly, the septum nasi is continuous with the sphenethmoid.

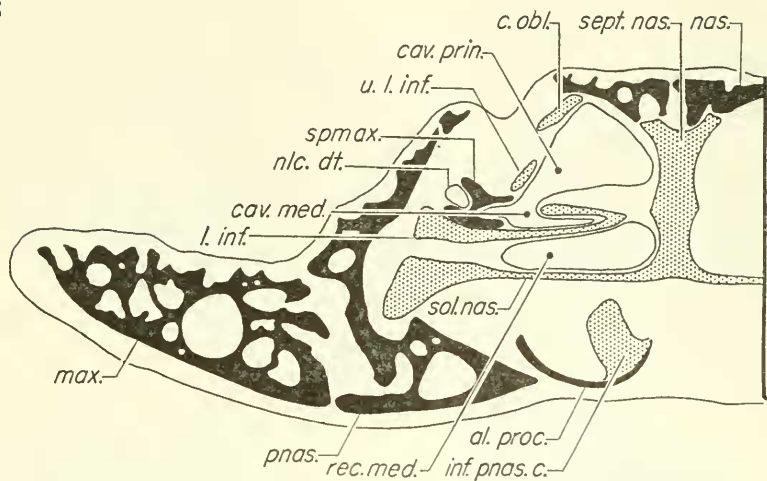
*Nasal cavities and associated structures.*—The cavum principale (*cav. prin.*) is the anteriormost to appear. The anterior end is bordered by the alary cartilage laterally, the tectum nasi dorsomedially, and the septum nasi medially. A short distance posterior to the anterior end of the cavum the external naris opens dorsally (Fig. 5). The cavum is supported ventrally by the solum nasi. The cavum principale extends posteriorly within the anterior recesses of the sphenethmoid to a level slightly anterior to the disappearance of the medial septum (Fig. 17).

The cavum medium (*cav. med.*) appears ventral to the cavum principale within the solum nasi. The anterior end of the cavum lies at a level just posterior to the appearance of the septomaxillary and the opening of the external naris, and anterior to the level of the foramen ramus externus narius and ramus medius narius (Fig. 5). The presence of the cavum differentiates the lamina superior (*l. sup.*) lying between the cavum principale and cavum medium, and the lamina inferior (*l. inf.*), lying ventral to the cavum medium (Figs. 6 and 7). As the cavum medium increases in width posteriorly, the laminae lose their lateral connection. The lateral part of the cavum medium diverges as the nasolacrimal duct (*nlc. dt.*, Fig. 8) at a level posterior to the external naris where the cavum medium joins the cavum principale. The cavum medium terminates near the posterior end of the septomaxillary.

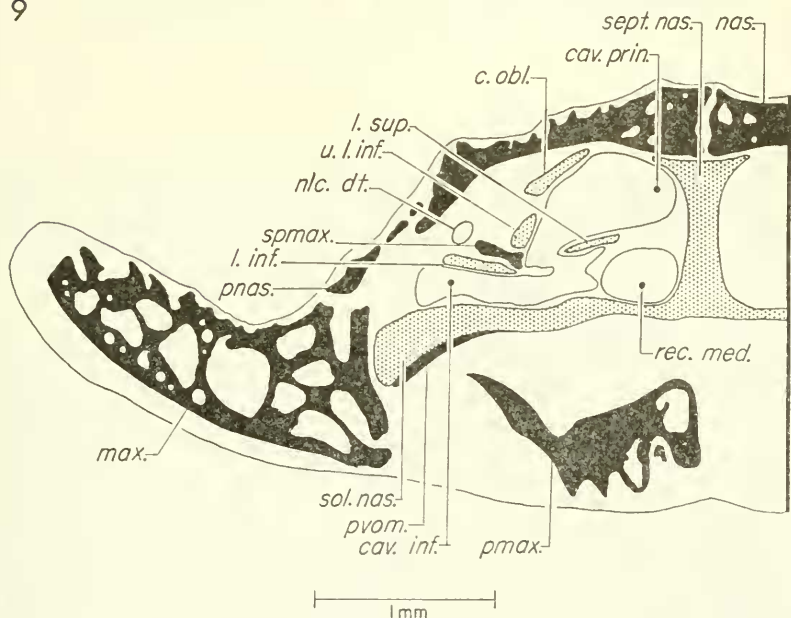
The anterior end of the recessus medialis (*rec. med.*) of the cavum inferius lies slightly posterior to the foramen of the ramus externus narius and ramus medius narius (Figs. 5-7). The presence of the recessus medialis differentiates the crista intermedia (*cr. int.*, Fig. 7) dorsally as a cartilaginous stalk joining the laminae superior and inferior to the septum nasi. Immediately anterior to the nasolacrimal duct the crista intermedia loses its medial connection to the septum nasi (Figs. 6 and 7 d-e); shortly thereafter the recessus medialis expands laterally to form the anterior part of the cavum inferius (*cav. inf.*, Fig. 8). In subsequent sections the crista intermedia gradually recedes laterally from the septum nasi, the cavum inferius grows larger, the solum nasi extends laterally to meet the maxillary, the prenasal disappears, and the pars dentalis of the premaxillary appears (Figs. 8 and 9). At the latter level the cavum principale is confluent with the recessus lateralis (*rec. lat.*) of the cavum inferius, whereas the recessus medialis has lost its connection with the recessus lateralis. Slightly posterior to the appearance of the prevomer, the recessus medialis disappears.

The crista subnasalis (*cr. sub.*, Fig. 11) differentiates from the lateral edge of the solum nasi. The crista lies adjacent to the maxillary in sections posterior to the recessus medialis. The crista subnasalis persists as a rod of cartilage, which gradually diminishes in diameter and finally terminates at the anterior limits of the olfactory eminence (Fig. 12).

8



9



FIGS. 8-9. Transverse sections through olfactory capsule of *Triprion petasatus* (KU 71745): (8) level of infundibulum; (9) level of recessus lateralis of cavum inferius. Abbreviations: *al. proc.*, alary process of premaxillary; *c. obl.*, cartilago obliquus; *cav. inf.*, cavum inferius; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *pmax.*, premaxillary; *pnas.*, prenasal; *pvom.*, prevomer; *rec. med.*, recessus medialis of cavum inferius; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary; *u. l. sup.*, upper part of lamina superior.

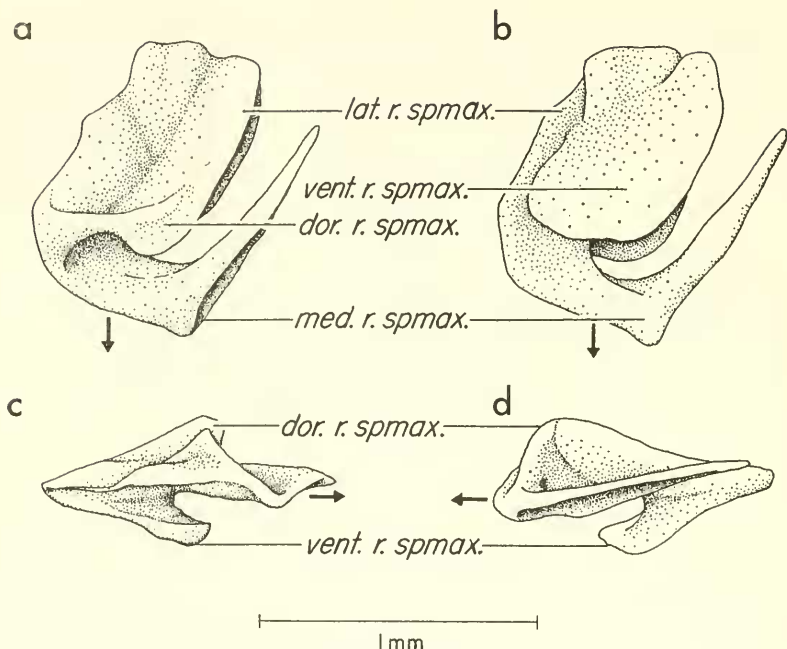
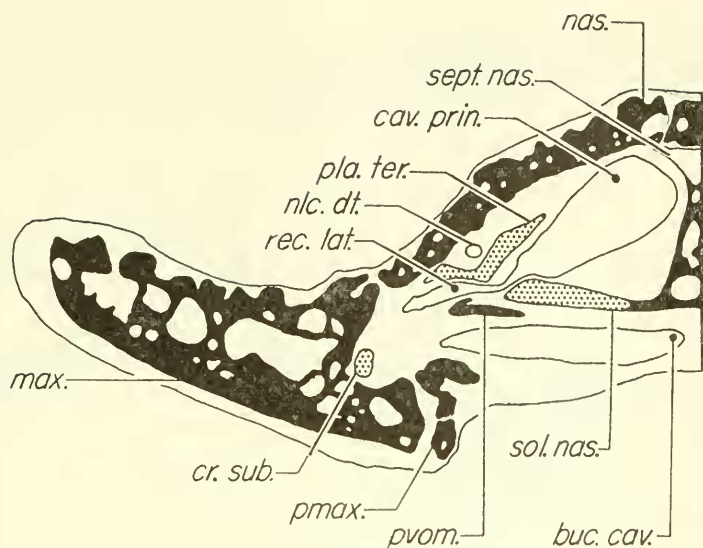


FIG. 10. Septomaxillary bone drawn from dried skeletal preparation of *Triprion petasatus* (KU 71759) ♂: (a) dorsal view; (b) ventral view; (c) lateral view; (d) medial view. Arrows indicate anterior ends. Abbreviations; *dor. r. spmax.*, dorsal ramus of septomaxillary; *lat. r. spmax.*, lateral ramus of septomaxillary; *med. r. spmax.*, medial ramus of septomaxillary; *vent. r. spmax.*, ventral ramus of septomaxillary.

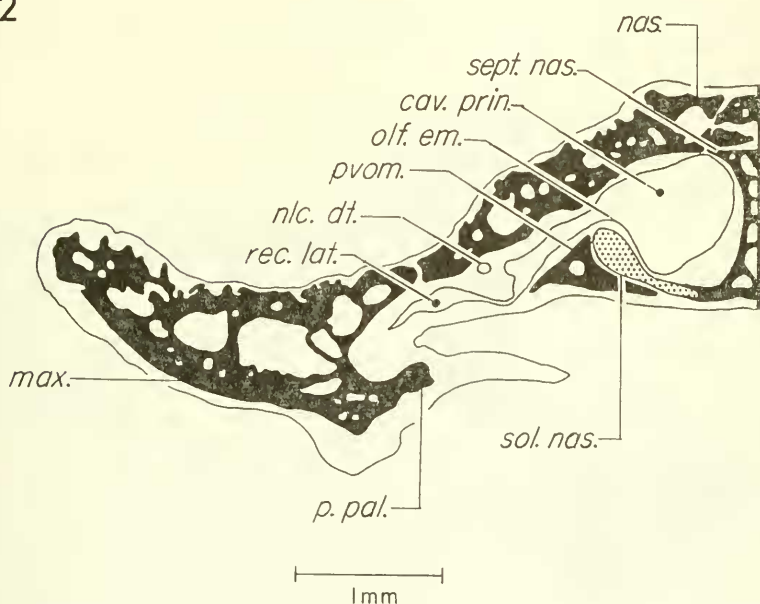
**Septomaxillary.**—The septomaxillary (*spmax.*, Fig. 10) first appears ventral to the alary cartilage as a small, horizontally-oriented bone overlying the lateral half of the anterior end of the cavum medium (Figs. 5 and 7 a-b). It gradually widens and just anterior to the recessus medialis becomes depressed medially and bifurcates (Fig. 7 c-d) into medial and lateral rami to accommodate the connection of the cavum principale with the cavum medium. A ventral ramus of the septomaxillary projects ventral to the cavum medium (Fig. 7e). Slightly posterior, the ventral ramus joins the dorsal ramus of the septomaxillary (Fig. 8), thereby separating the main part of the cavum medium from its lateral part. The latter is the anterior end of the nasolacrimal duct. Posteriorly, the septomaxillary gradually reduces in size. The medial branch terminates just as the recessus medialis joins the recessus lateralis; the lateral branch terminates slightly posterior to the medial branch.

**Planum Terminale.**—The cartilago obliquus (*c. obl.*) maintains its dorsolateral position posterior to the appearance of the recessus medialis (Fig. 6). Posterior to the infundibulum and septomaxillary, at the level of the confluence of the cava principale and medium, the dorsolateral remnant of the lamina inferior joins the cartilago obliquus to form the anterior end of the planum terminale (*pla. term.*, Fig. 11). The planum is arcuate in cross-section, narrow dorsally, and broad

11



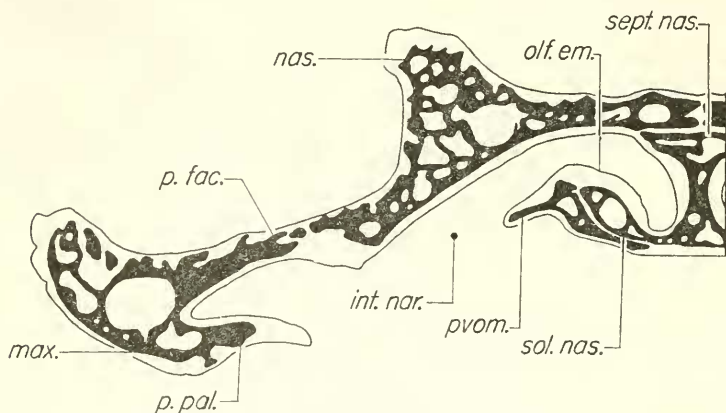
12



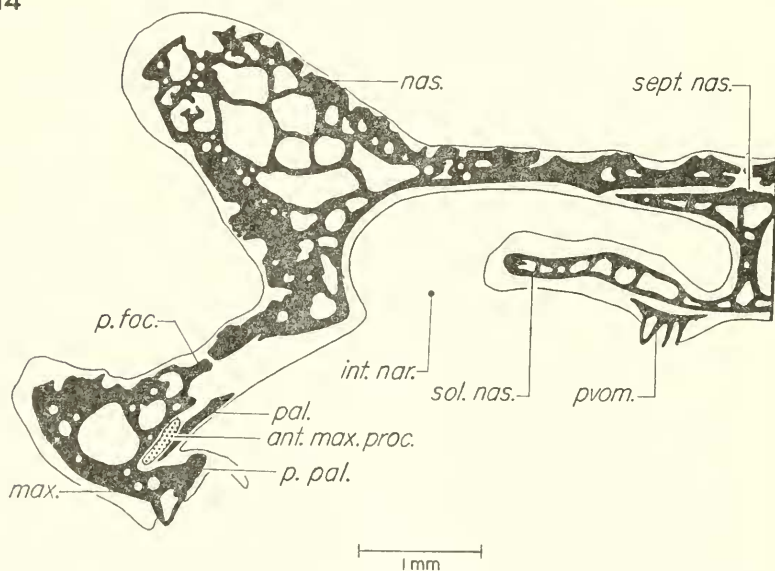
FIGS. 11-12. Transverse sections through posterior part of olfactory capsule of *Triprion petasatus* (KU 71745): (11) level of planum terminale; (12) anterior level of olfactory eminence. Abbreviations: *buc. cav.*, buccal cavity; *cav. prin.*, cavum principale; *cr. sub.*, crista subnasalis; *max.*, maxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *olf. em.*, olfactory eminence; *p. pal.*, pars palatina of maxillary; *pla. term.*, planum terminale; *pmax.*, premaxillary; *pvom.*, prevomer; *rec. lat.*, recessus lateralis of cavum inferius; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi.

ventrally and lies lateral to the cavum principale. In subsequent sections the planum is reduced in width and then expanded ventrolaterally to form a lateral ledge of cartilage separating the nasolacrimal duct from the recessus lateralis.

13



14



FIGS. 13-14. Transverse sections through skull of *Triprion petasatus* (KU 71745) at level of olfactory eminence: (13) anterior level of internal nares; (14) level of palatine bone. Abbreviations: *ant. max. proc.*, anterior maxillary process; *int. nar.*, internal nares; *max.*, maxillary; *nas.*, nasal; *olf. em.*, olfactory eminence; *p. fac.*, pars facialis; *p. pal.*, pars palatina; *pal.*, palatine; *pvom.*, prevomer; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi.

At the anterior edge of the olfactory eminence the planum terminale is restricted to a dorsal strip of cartilage lying medial to the nasolacrimal duct, between the nasal bone and the cavum principale. It gradually diminishes in size posteriorly and disappears anterior to the opening of the internal naris.

*Anterior and Posterior Maxillary Processes.*—The anterior terminus of the anterior maxillary process (*ant. max. proc.*) lies in the medial part of the maxillary at a level just posterior to the opening of the internal naris. In subsequent sections the process extends medially, out of the maxillary, and then dorsally along the medial face of the pars facialis and the nasal bone in the region of the palatine (Fig. 14). In sections immediately posterior to the internal naris, the anterior process meets the beginning of the transition zone between the solum nasi and the planum antorbitale (*pla. ant.*, Fig. 15). Posterior to the zone of transition and the disappearance of the planum antorbitale, the anterior maxillary process is replaced by the posterior maxillary process (*post. max. proc.*). The latter is a small rod of cartilage between the pars palatina and pars facialis of the maxillary (Fig. 17-19). Posteriorly, the cartilage is associated with the pterygoid as the pterygoid process (*pter. proc.*, Fig. 20).

*Planum Antorbitale.*—The planum antorbitale (*pla. ant.*) appears adjacent to medial face of the nasal, posterior to the closing of the internal naris. It is a small structure which united the tectum dorsally and the solum nasi and anterior maxillary process ventrally (Figs. 15 and 16). Posterior to this fusion, the cartilage is replaced by the bony sphenethmoid, leaving only a small dorsolateral remnant of the planum antorbitale which quickly diminishes and disappears.

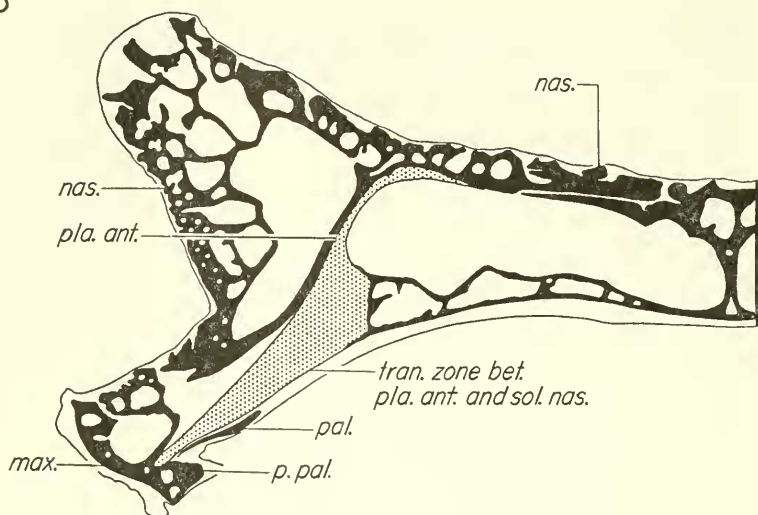
### The Sphenethmoid and External Dermal Bones Associated with the Sphenethmoid Region

The frontoparietal (*fpar.*), the sphenethmoid (*spheth.*), and the anterior part of the parasphenoid (*prsph.*) are included in the sphenethmoid region.

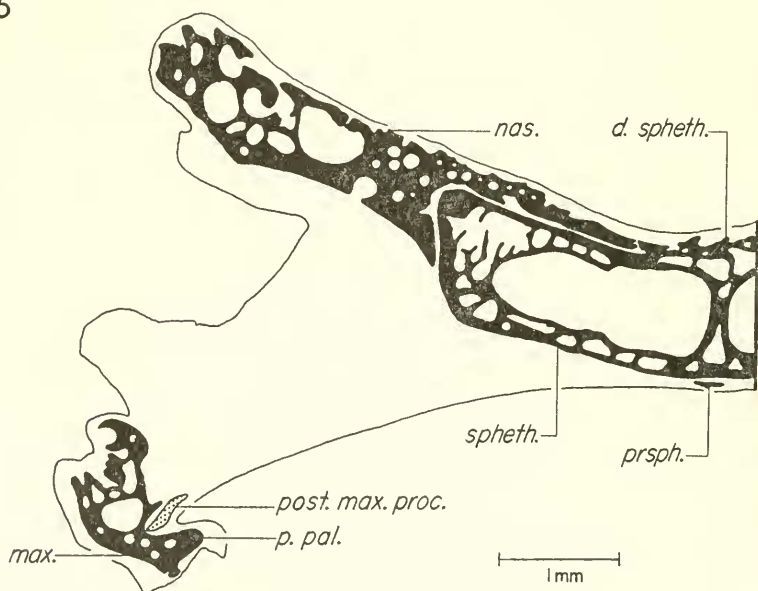
*Frontoparietal.*—The frontoparietal (*fpar.*, Pl. 2a; Fig. 1b) is an approximately rectangular-shaped element which articulates anterolaterally with the posterior margin of the nasal and anteromedially with the posterior margin of the dermal sphenethmoid. Laterally, the frontoparietal extends over the orbit as a bony shelf; posterolaterally it is attached to the squamosal. The posterior margin of the frontoparietal terminates in an upturned flange (Pls. 2a and 3a) referred to as the occipital crest. Ventral to the occipital crest, the frontoparietal is attached, but not fused, to the exoccipital (Pl. 3b). Posterior to the dermal sphenethmoid the frontoparietals converge. The dorsal surface of the frontoparietal is involved in integumentary-cranial co-ossification. Like the nasal, the frontoparietal is characterized by bony striations which form a radiate pattern centered at the mid-length of the bone slightly lateral to the mid-width. The striations are most prominent anteriorly and medially over the orbit, and posteriorly on the margin of the occipital crest where they terminate in spinose processes.

*Sphenethmoid.*—The dermal sphenethmoid (*d. spheth.*, Pl. 2a; Fig. 1b) is a diamond-shaped bone occupying the depressed central region of the skull. The anterolateral margins of the dermal sphenethmoid articulate with the posteromedial edges of the nasals, and the posterolateral margins of the bone with the anteromedial edges of the frontoparietals. The dermal sphenethmoid is com-

15



16



FIGS. 15-16. Transverse sections through skull of *Triprion petasatus* (KU 71745) at anterior level of sphenethmoid: (15) level of planum antorbitale; (16) anterior end of parasphenoid. Abbreviations: *d. spheth.*, dermal sphenethmoid; *max.*, maxillary; *nas.*, nasal; *p. pal.*, pars palatina of maxillary; *pal.*, palatine; *pla. ant.*, planum antorbitale; *post. max. proc.*, posterior maxillary process; *prsph.*, parasphenoid; *spheth.*, sphenethmoid; *tran. zone bet. pla. and sol. nas.*, transition zone between planum antorbitale and solum nasi.

pletely involved in integumentary-cranial co-ossification and is marked by a centrally located, radiate pattern of striations. The dorsally-exposed dermal sphenethmoid is confluent with the underlying endochondral sphenethmoid as described in *Hyla septentrionalis* (Trueb, 1966).

The endochondral sphenethmoid (*spheth.*, Fig. 1b) is an extensive element which is completely covered dorsally by the dermal roofing bones. The sphenethmoid is in synchondrotic continuity with the septum nasi; thus, in ventral view (Pl. 2b) it appears to originate anteriorly in a pointed process dorsal to the palatine processes of the premaxillaries. The floor of the sphenethmoid widens posteriorly, forming the posteromedial and posterior margins of the internal nares. Posterior to the palatines, the venter of the sphenethmoid reaches its widest extent and attaches to the medial surface of the nasals anterior to the orbit. The sphenethmoid narrows abruptly in the anterior region of the orbit and posteriorly narrows more gradually to its terminus at the foramen of the optic nerve.

*Parasphenoid.*—The parasphenoid (*prspth.*, Pl. 2b) is a long, delicate bone which lies on the ventromedial surfaces of the sphenethmoid and prootics. The narrow, anterior end of the parasphenoid lies just posterior to the prevomer. The bone widens posteriorly, but is medially constricted in the region of the sphenethmoid-prootic junction; it abruptly widens ventral to the prootic and then narrows to a terminal point, which lies just anterior to the foramen magnum. The parasphenoid bears an odontoid-like structure in the form of an irregular, thin, ventral projection (Pl. 3a), which extends from a point just posterior to the level of the orbitonasal foramen to the posterior edge of the orbit.

### Internal Bones and Cartilages of the Sphenethmoid Region

The synchondrotic union of the septum nasi and the sphenethmoid precludes a clear distinction between the olfactory and sphenethmoid regions. Generally the posterior border of the internal naris is a convenient point to terminate description of the olfactory region. However, in *Triprion* the dermal sphenethmoid and palatine are present anterior to this point, and the septum nasi and cavum principale posterior to it. The anterior end of the sphenethmoid region is arbitrarily established at the level of the union of the solum nasi with the planum antorbitale posterior to the internal naris (Fig. 15).

*Sphenethmoid.*—At the anterior end of the sphenethmoid (Figs. 15 and 16), the bone is divided medially by a bony partition which is continuous with the septum nasi anteriorly. The only cartilage associated with the sphenethmoid at this level is a small dorsolateral remnant of the planum antorbitale; the latter disappears in sections just anterior to the orbitonasal foramen. Immediately posterior to the orbitonasal foramen the medial septum of the sphenethmoid terminates (Fig. 18). At this level a small amount of cartilage is located at the distal tip of the anterolateral wing of the sphenethmoid underlying the nasal; the rest of the sphenethmoid is bony. In subsequent sections, the cartilage disappears as the lateral wings of the sphenethmoid diminish in size (Fig. 19). Just posterior to the end of the dermal sphenethmoid, the roof of the sphenethmoid splits beneath the frontoparietals to form the frontoparietal fontanelle (*fpar. fon.*, Fig. 20). Anterior to the optic foramen the taenia tecta marginalis (*t. t. mar.*, Fig. 20) appears dorsally, and the sphenethmoid is re-

stricted to form the bony, V-shaped floor of the neurocranium. Immediately anterior to the optic foramen, the ventral part of the sphenethmoid is replaced by cartilage joining the sphenethmoid and prootic.

Because of the unusual dual nature of the sphenethmoid and the size of the nasals and frontoparietals, a brief description of the internal relations of these bones is included. The anterior end of the dermal sphenethmoid appears dorso-medially between the nasals at the level of the transition zone between the solum nasi and planum antobitale (Fig. 15). The dermal and endochondral sphenethmoid are continuous and, as a unit, both are separated from all adjacent elements by connective tissue. The dermal sphenethmoid attains its maximum width in the mid-orbital region (Fig. 18) at the articulation between the nasal and frontoparietal. This articulation is not a simple juxtaposition. The frontoparietal bears an anterior flange which underlies the posterior margin of the nasal (Fig. 18). At the posterior terminus of the dermal sphenethmoid, the frontoparietals converge medially over the endochondral sphenethmoid (Fig. 20). In subsequent sections the endochondral sphenethmoid diverges medially to form the frontoparietal fontanelle. The frontoparietal overlying the fontanelle is noticeably thicker than the same bone in previous sections; perhaps this is a structural compensation for the loss of the underlying sphenethmoid. The fontanelle is covered by connective tissue continuous with that separating the sphenethmoid and frontoparietal anteriorly and laterally.

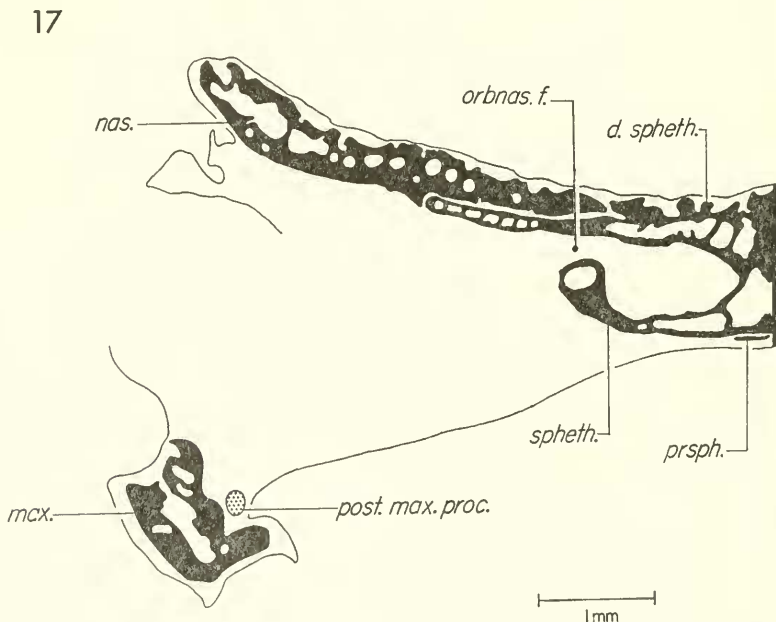
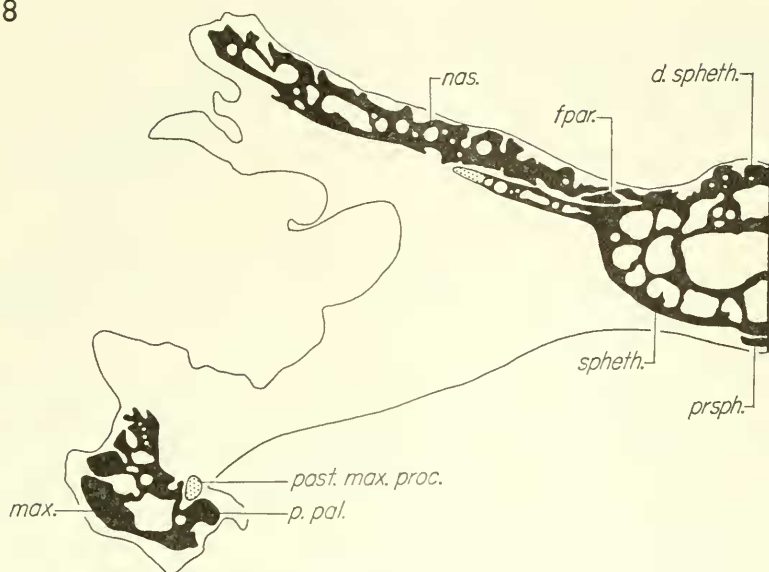
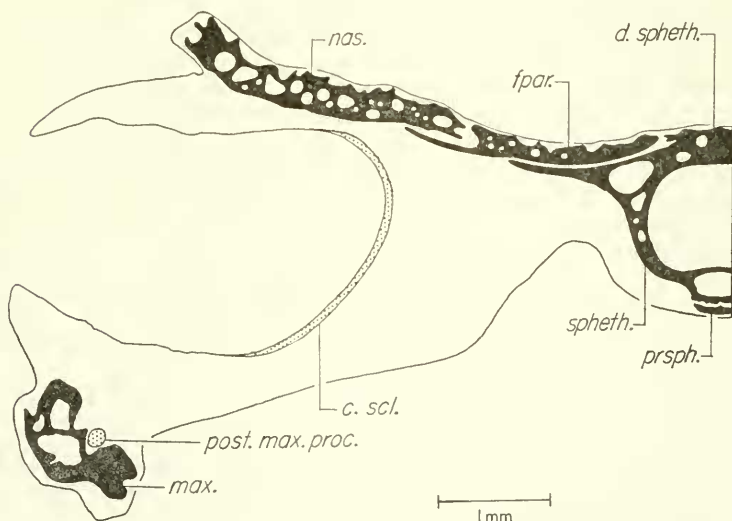


FIG. 17. The transverse section through skull of *Tripurion patasatus* (KU 71745) at level of orbitonasal foramen. Abbreviations: *d. spheth.*, dermal sphenethmoid; *max.*, maxillary; *nas.*, nasal; *orbnas. f.*, orbitonasal foramen; *post. max. proc.*, posterior maxillary process; *prspsh.*, parasphenoid; *spheth.*, sphenethmoid.

18



19



FIGS. 18-19. Transverse sections through skull in orbital region of *Triprion petasatus* (KU 71745) showing relationships of sphenethmoid, nasal, and frontoparietal: (18) anterior level of frontoparietal; (19) posterior level of nasal. Abbreviations: *c. scl.*, cartilaginous sclera; *d. spheth.*, dermal sphenethmoid; *fpar.*, frontoparietal; *max.*, maxillary; *nas.*, nasal; *p. pal.*, pars palatina of maxillary; *post. max. proc.*, posterior maxillary process; *prsph.*, parasphenoid; *spheth.*, sphenethmoid.

*Parasphenoid*.—The parasphenoid (*prsp.*, Figs. 16-27) is a delicate bone which lies ventral to the endochondral sphenethmoid. The parasphenoid is separated from adjacent bones by connective tissue and generally conforms in shape to the floor of the neurocranium.

*Orbitonasal Foramen*.—The orbitonasal foramen (*orbnas. f.*, Fig. 17) is present in sections just anterior to the posterior end of the medial sphenethmoid septum. The foramen is completely bordered by bone and lies in the dorso-lateral corner of the neurocranium.

### External Bones of the Orbital, Otic, and Occipital Regions

The squamosal, pterygoid, quadratojugal, and posterior part of the the frontoparietal and parasphenoid are included as external bones of the orbital, otic, and occipital regions. The external relations of the frontoparietal and parasphenoid have been described in the previous section.

*Frontoparietal*.—The frontoparietal (Pl. 2a; Fig. 1b) completely covers the orbital and otic regions; it is separated from the underlying exoccipital by a layer of connective tissue. The frontoparietal spans the prootic (Pl. 3b; Figs. 24 and 25), thereby providing space for the attachment of the adductor mandibulare anterior and posterior muscles to the dorsum of the prootic and to the lateral regions of the exoccipital; the posterolateral corner of the frontoparietal attaches to the head of the squamosal.

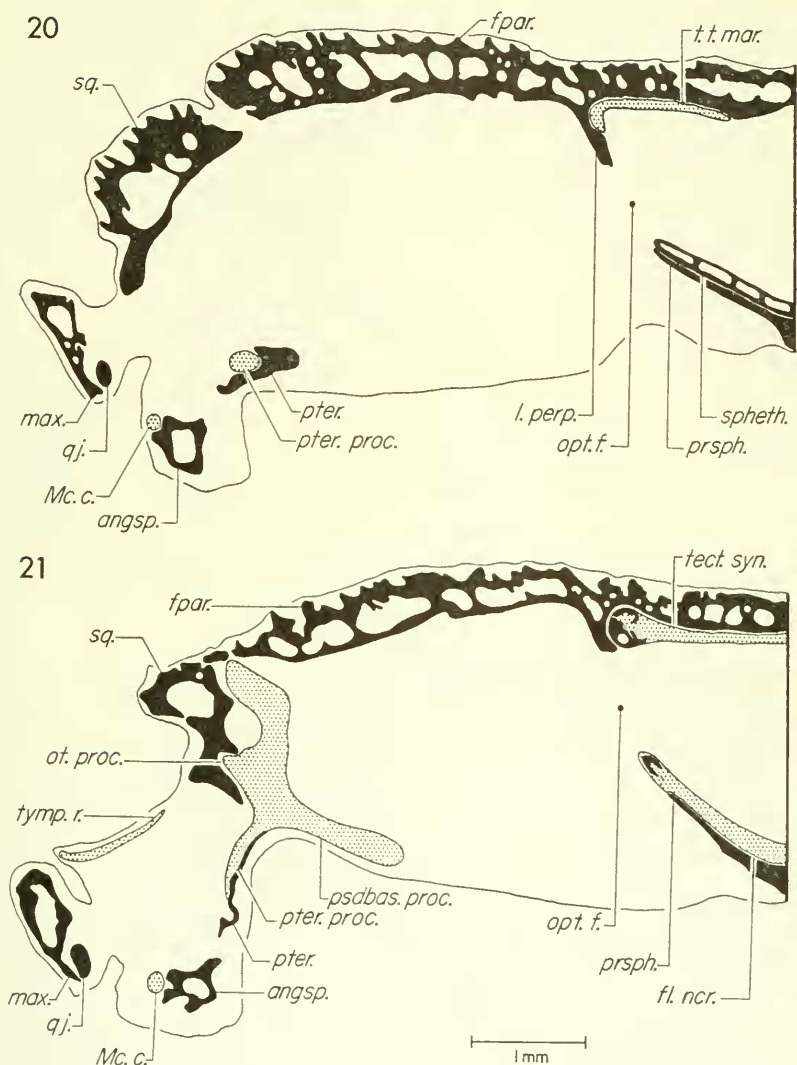
*Squamosal*.—In dorsal view the squamosal (*sq.*, Pl. 2a) is an arcuate bone which extends posteriorly from the posterior edge of the orbit to the level of the occipital crest. The dorsal and dorsolateral surfaces of the head of the squamosal are completely involved in integumentary-cranial co-ossification. The anterior arm of the squamosal is robust (Pl. 3a) and forms the posterior margin of the orbit and terminates ventrally on the medial edge of the maxillary. The posterior arm is as robust as the anterior arm and bears a heavy tendinous connection to the quadratojugal ventrally. The ventral arm of the squamosal extends posteroventrally from the mid-point of the arc formed by the anterior and posterior arms of the squamosal.

*Pterygoid*.—The pterygoid (Pl. 2b; Fig. 1b) is moderately robust but small. The anterior ramus attaches to the pars dentalis of the maxillary just anterior to the maxillary-quadratojugal articulation. The posterior ramus articulates with the quadrate process in the articular region of the skull. The medial ramus is reduced and does not articulate with the prootic.

*Quadratojugal*.—The well developed quadratojugal (Pls. 2b and 3a) articulates with the quadrate process and ventral arm of the squamosal medially and with the maxillary laterally and anteriorly. The quadratojugal lies adjacent to the maxillary in the recess formed by the pars facialis and pars palatina of the maxillary. The anterior end of the quadratojugal articulates with the posterior end of the pars dentalis of the maxillary.

### Internal Bones and Cartilages of the Orbital, Otic, and Occipital Regions

*Nerve Foramina of the Orbital, Otic, and Occipital Regions*.—The optic foramen (*opt. f.*, Figs. 20 and 21) has a complete, bony margin; the anterior and ventral edges are formed by peripheral ossification of the sphenethmoid, the dorsal margin by the prootic. The trochlear foramen (*troc. f.*) lies just



FIGS. 20-21. Transverse sections through skull of *Triprion petasatus* (KU 71745) at level of optic foramen; (20) anterior level of optic foramen; (21) posterior level of optic foramen. Abbreviations: *angsp.*, angulosplenial; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *l. perp.*, lamina perpendicularis of frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *opt. f.*, optic foramen; *ot. proc.*, otic process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *qj.*, quadratojugal; *spheth.*, sphenethmoid; *sq.*, squamosal; *t. t. mar.*, taenia tecti marginalis; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

posterior and dorsal to the optic foramen. Slightly posterior and ventral to the optic foramen, the oculomotor foramen (*ocul. f.*, Fig. 22) appears in the prootic bone. The foramen bears a complete bony margin and is only narrowly separated posteriorly from the large prootic foramen (*pro. f.*, Fig. 23) housing the ganglion prootic commune and abducens nerve. Considerably posterior, at the level of the operculum (*op.*, Fig. 26), the anterior acoustic foramen (*ant. acus. f.*) appears. It is separated by a narrow region of cartilage from the posterior acoustic foramen (*post. acus. f.*, Fig. 27). A narrow bridge of bone separates the posterior acoustic foramen from the more ventral jugular foramen (*jug. f.*, Fig. 28). Slightly posterior and lateral to the latter, the foramen perilymphaticum appears.

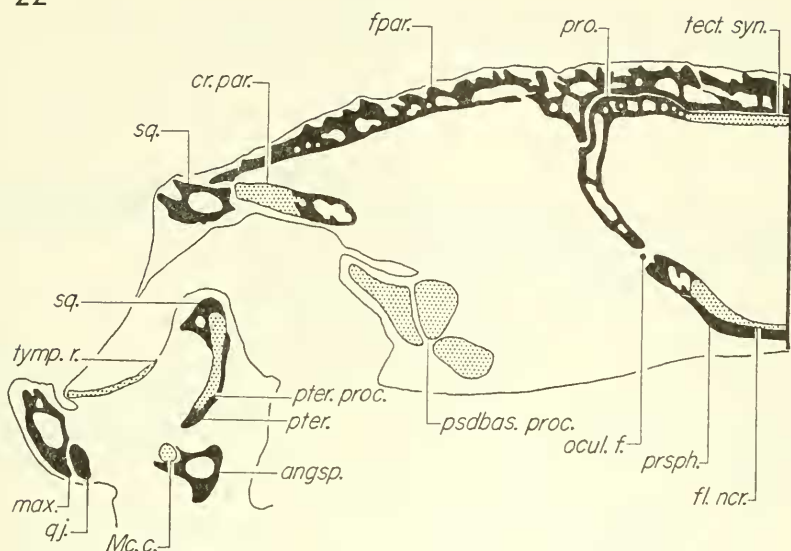
*Otic Region.*—The otic process (*ot. proc.*) first appears at the level of the optic foramen, posterior to the entry of the optic nerve into the neurocranium. Initially the oval cartilage is encased in the head of the squamosal. The process lengthens and comes to lie medial to the squamosal head. Somewhat posteriorly (Fig. 21), the otic process fuses ventrally with the pterygoid and pseudobasal processes. Just anterior to the oculomotor foramen, the otic process loses its connection with the ventral cartilages and assumes a horizontal position as the crista parotica (*cr. par.*, Figs. 22-25). The crista parotica joins the ossified prootic medially. The pterygoid process loses its connection with the pseudobasal process and the cornu principalis of the hyale (*corn. prin.*, Figs. 23 and 24) diverges laterally from the pseudobasal process. The pseudobasal process is short; it coalesces after a short distance with the ventrolateral ledge of the otic capsule medially (*vl. l. ot. c.*, Figs. 23 and 24).

At the level of the prootic foramen (Fig. 23) the cornu principalis is restricted ventrally; the pars externa plectri (*p. ext. pl.*) has appeared laterally and the pars media plectri (*p. med. pl.*) at the ventrolateral tip of the otic capsule. The pars externa plectri is joined to the crista parotica for a short distance by the pars ascendens plectri (*p. asc. pl.*). The cornu principalis extends posteroventrally from the pseudobasal process and terminates just anterior to the fenestra ovalis. The pars interna plectri (*p. int. pl.*, Fig. 25) lies in the fenestra ovalis at the level of the anterior acoustic foramen. The operculum (*op.*, Fig. 26) appears immediately lateral to the pars interna plectri as a small crescent-shaped cartilage. The pars interna plectri disappears and the operculum effects the lateral closure of the fenestra ovalis, uniting the dorsal and ventral components of the otic capsule at the level of the posterior acoustic foramen. Anterior to the closure of the foramen the operculum disappears.

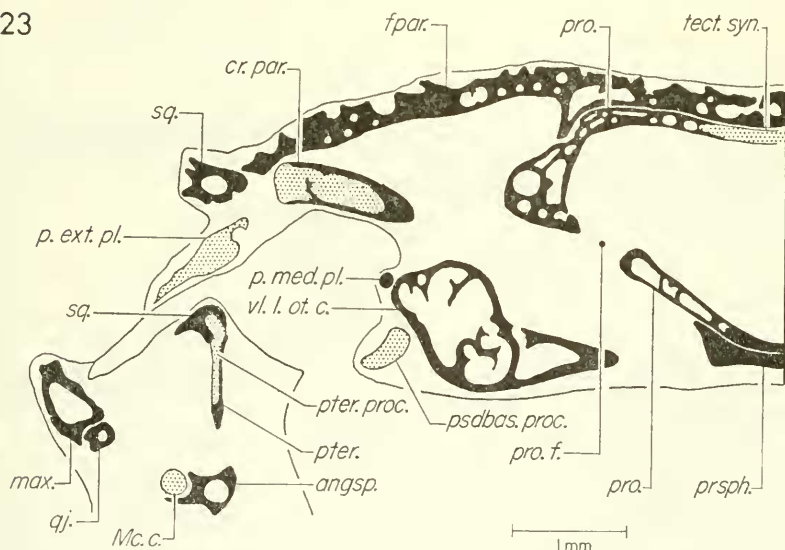
*Pterygoid.*—The pterygoid appears at the mid-level of the orbit and invests the pterygoid process dorsomedially. At subsequent levels the pterygoid extends posteromedially toward the ventrolateral ledge of the otic capsule (Figs. 20-23). The bony medial ramus of the pterygoid does not meet the otic capsule, although the pterygoid process fuses with the ventral block of cartilage which gives rise to the cornu principalis and pseudobasal process. In more posterior sections, the pterygoid is present as a thin, bony element which invests the medial side of the pterygoid and quadrate processes and lies medial to the ventral arm of the squamosal. The pterygoid extends posterior to the posterior termini of the quadratojugal and angulosplenic bones.

*Ossification in the Otic and Occipital Regions.*—At the posterior level of the optic foramen (Fig. 21) the floor of the neurocranium (*fl. ncr.*) is only peripherally ossified; likewise the roof, the tectum synoticum, is peripherally ossified.

22

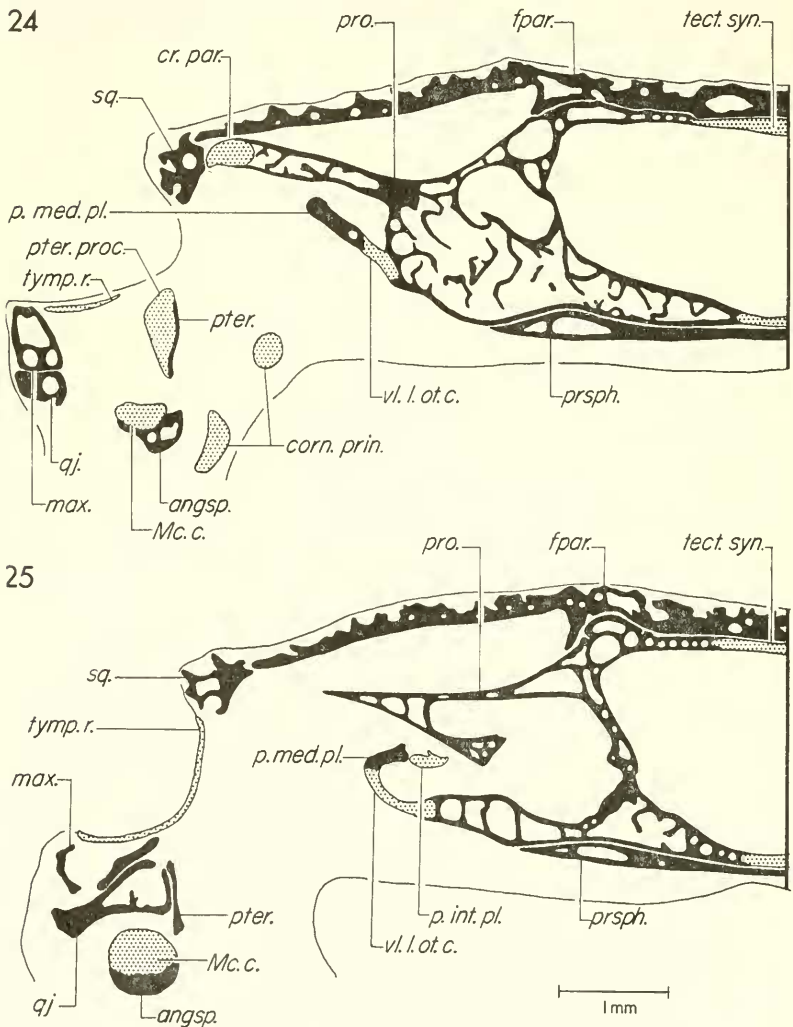


23



FIGS. 22-23. Transverse sections through skull of *Triprion petasatus* (KU 71745) at anterior level of otic region: (22) level of oculomotor foramen; (23) level of prootic foramen. Abbreviations: *angsp.*, angulosphenial; *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *ocul. f.*, oculomotor foramen; *p. ext. pl.*, pars externa plectri; *p. med. pl.*, pars media plectri; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring; *vl. l. ot. c.*, ventrolateral ledge of otic capsule.

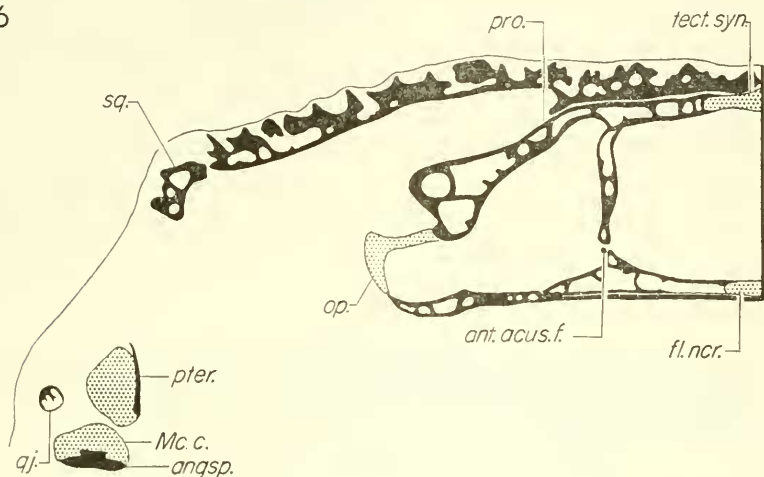
The ventral cartilage presumably represents the junction between the sphenethmoid and prootic bones. Ossification increases posteriorly in the walls of the neurocranium; at the posterior limits of the skull only a small mid-ventral



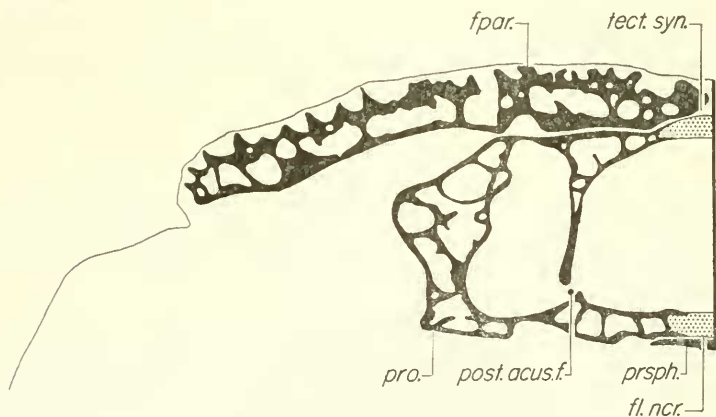
FIGS. 24-25. Transverse sections through otic region of skull of *Triprior petasatus* (KU 71745): (24) level of pars media plectri; (25) level of pars interna plectri. Abbreviations: *angsp.*, angulosplenic; *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring; *vl. l. ot. c.*, ventrolateral ledge of otic capsule.

section of the exoccipital remains cartilaginous (Fig. 28). The otic capsule is almost entirely ossified with the exception of its ventrolateral ledge (Figs. 24 and 25), which is cartilaginous. The pars media plectri is totally ossified, but the crista parotica, pars externa plectri, pars ascendens plectri, pars interna plectri, and operculum are cartilaginous.

26



27



1 mm

FIGS. 26-27. Transverse sections of skull of *Tripurion petasatus* (KU 71745) through posterior part of otic region: (26) level of anterior acoustic foramen; (27) level of posterior acoustic foramen. Abbreviations: *angsp.*, angulosplenial; *ant. acus. f.*, anterior acoustic foramen; *fl. ncr.*, floor of neurocranium; *Mc. c.*, Meckel's cartilage; *op.*, operculum; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *sq.*, squamosal; *tect. syn.*, tectum synoticum.

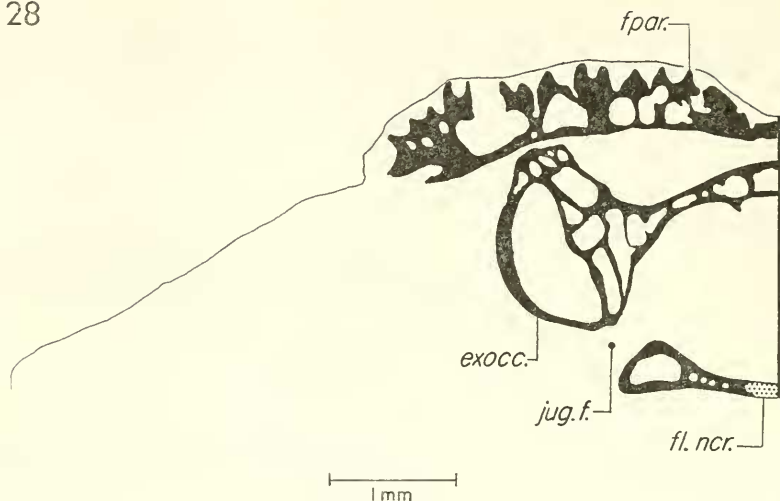


FIG. 28. Transverse section of skull of *Tripriorion petasatus* (KU 71745) at level of jugular foramen. Abbreviations: *exocc.*, exoccipital; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *jug. f.*, jugular foramen.

### The Bursa Angularis Oris

The bursa angularis oris (*b. ang. o.*, Fig. 29) is present as a mass of lymphoid tissue between the maxillary and pterygoid bones in the posterior part of the orbit. The bursa lacks organized glandular structure and distinct boundaries; it has no lumen and is separated from the oral cavity by cuboidal ciliated epithelium.

### The Articular Region

Anterior to the articular region, Meckel's cartilage is small and lies dorso-lateral to the angulosplenic bone. Posteriorly, it enlarges and takes a dorsal position with respect to the angulosplenic while the latter assumes a shallow crescentic shape.

The quadratojugal first appears in sections just posterior to the orbit. From an initial position medial to the maxillary the quadratojugal enlarges posteriorly and moves to a position ventral to the maxillary, while the latter decreases in size. The quadratojugal later joins the quadrate process medially. Perichondral and endochondral ossification of this element persists posterior until the loss of the angulosplenic; thereafter the posterior quadrate process articulates with Meckel's cartilage. Both elements disappear at the posterior level of the posterior acoustic foramen.

### Summary of the Description of the Skull of *Tripriorion*

1. All dorsal and lateral parts of the skull are involved in integumentary-cranial co-ossification. Dermal roofing bones are extensive and form a complete casque, or cranial roof. The skull is

distinguished by spinose maxillary and prenasal flanges, a spinose preorbital knob, transverse rows of spines across the occipital region, and ornate sculpturing of all dorsal and lateral surfaces of dermal bones.

2. A dermal sphenethmoid and prenasal are present.

3. Most of the septum nasi and part of the solum nasi are ossified. The olfactory eminence is supported by a cartilaginous part of the solum nasi and by the bony prevomer.

4. Both the inferior and superior prenasal cartilages are present.

5. The lingual process is absent and there is no palatal cartilage isolated between the maxillaries.

6. The anterior end of the cavum medium lies anterior to the cavum inferius.

29

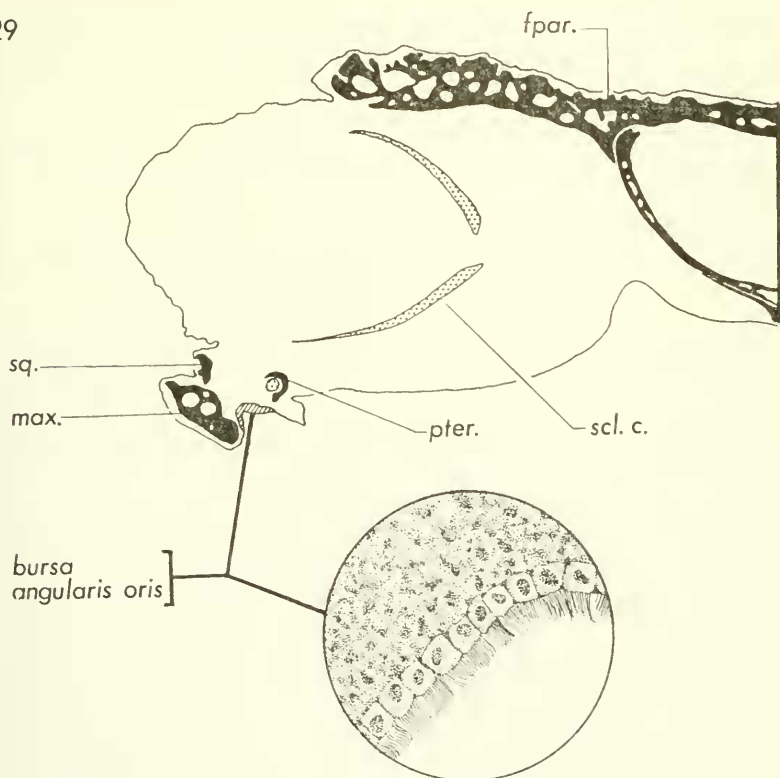


FIG. 29. Transverse section of skull of *Triprion petasatus* (KU 71745) in orbital region at level of bursa angularis oris. Inset shows enlargement ( $\times 570$ ) of bursa angularis oris. Abbreviations: *fpar.*, frontoparietal; *max.*, maxillary; *pter.*, pterygoid; *scl. c.*, cartilaginous sclera; *sq.*, squamosal.

7. The septomaxillary is basically a U-shaped structure which has a shallow dorsal ramus and ventral ramus on the lateral branch.
8. A distinct pars nasalis is absent on the maxillary.
9. The palatine is reduced to a small, flat, rectangular bone which lies adjacent to the maxillary.
10. A cartilaginous sclera is present.
11. Remnants of the taenia tecti marginalis and tectum synoticum are evident in the adult.
12. The external part of the plectral apparatus (the columella) is directed anterolaterally. The pars ascendens is fused with the crista parotica.
13. The pseudobasal process is fused to the otic capsule.
14. The cornu principalis of the hyale is fused with the pseudo-basal process.
15. Two acoustic foramina are present.
16. The sphenethmoid and prootic are synchondrotically united.
17. The frontoparietal is separate from the prootic and exoccipital.
18. The prootic and exoccipital are fused.
19. The medial ramus of the pterygoid does not articulate with the prootic.
20. A bursa angularis oris is present.

COMPARISON OF THE CRANIAL MORPHOLOGY OF  
*Triprrion petasatus* AND *Smilisca baudini*

The principal reason for selecting *Smilisca baudini* for comparison with *Triprrion* is that the cranial morphology of *S. baudini* seems to be unspecialized, even generalized, when compared with that of other hylids. *Smilisca* shows neither the loss of bones and reduction of ossification, nor the specialization of added bones and dermal ornamentation characteristic of some hylids.

With some exceptions, the cranial characters of hylids seem to be correlated with either habitat or size, or both. Loss of elements and reduction in ossification are generally characteristic of smaller frogs and/or frogs that breed in lotic situations, as opposed to the moderate-sized lentic breeders such as *Smilisca baudini*. *Hyla microcephala*, *H. eximia*, *H. phlebodes*, and *H. elaeochroa* are a few examples of small lentic breeders. These frogs show a reduction of ossification and a tendency toward loss of cranial elements as compared with *S. baudini*. The skull is poorly roofed; the frontoparietal fontanelle is characteristically large; the anterior arm of the squamosal is not in contact with the maxillary; the quadratojugal-max-

illary articulation is weak or absent; the pars facialis of the maxillary is reduced, and the nasal often lacks a maxillary process. The same kinds of reduction are characteristic of smaller lotic-breeding hylids, such as *Smilisca sordida*, *Hyla uranochroa*, *H. legleri*, *H. rufoculis*, *H. lancasteri*, and members of the genus *Ptychohyla*. The reduction or complete loss of the quadratojugal is especially marked among the smaller stream-breeders.

Larger lotic-breeding hylid frogs such as *Hyla chaneque*, *H. taeniopus*, *Plectrohyla*, and members of the *Hyla bistincta* group have more massive skulls than their smaller counterparts, but probably this cranial massiveness is attained secondarily. All of these frogs have frontoparietal fontanelles, and some lack a quadratojugal. The squamosal varies in size, but in none is it in contact with the maxillary. The nasal usually lacks a strong maxillary process, but in almost all of these frogs the pars facialis of the maxillary has a strong posterior process, which probably complements the function of the maxillary process of the nasal. The foregoing characters suggest that the crania of the lotic-breeding hylid frogs have evolved from a more generalized lentic ancestor, conceivably a frog having a cranium resembling that of *Smilisca baudini*. Smaller lentic and lotic hylids have reduced amounts of bone in their skulls. Perhaps this evolutionary pattern corresponds to a reduced need for protection and support; more likely, the meagerly ossified skulls are the result of arrested development.

Large lentic-breeding frogs, such as *Hyla boans*, *H. rosenbergi*, and *Phrynohyas*, tend to have more solidly roofed skulls than *Smilisca baudini*. A strong articulation exists between the quadratojugal and maxillary, and the frontoparietal fontanelle is absent in some, but in none does the squamosal articulate with the maxillary.

Apart from these general patterns, there are some bizarre cranial modifications among the hylids, exemplified by such frogs as *Anotheca coronata* and frogs of the genus *Hemiphractus*. The skull of *Anotheca* is characterized by spines along the canthal ridge, the edge of the frontoparietal over the orbit, across the occipital ridge, and on the anterior and posterior arms of the squamosal. Except for the extensive development of the frontoparietals, nasals, and pars facialis of the maxillary, the basic structure of the skull is similar to that of *Smilisca baudini*. However, *Hemiphractus* is markedly different from the majority of hylids. The skull is triangular in shape and characterized by large nasals and frontoparietals which completely roof the top of the skull. The massive squamosals are in

contact with the maxillaries anteriorly, and posteriorly in association with the frontoparietals, form posterolateral wings to the skulls. The skull is further distinguished by large prevomers, palatines and pterygoids, and a small prootic region.

Some of the most remarkable cranial modifications have taken place among frogs such as *Tripriion*, in which the cranial integument is co-ossified with the underlying bone. Included in this group are the genera *Trachycephalus*, *Osteocephalus*, *Pternohyla*, *Tripriion*, *Aparasphenodon*, *Corythomantis*, *Anotheca*, *Amphignathodon*, *Nyctimantis*, some members of the genus *Gastrotheca*, *Hyla septentrionalis*, *H. brunnea*, *H. dominicensis*, and *H. lichenata*. The basic architecture of the skulls of all these species is not unlike that of *Smilisca baudini*. However, their external appearances have been greatly altered by the extensive development of the dermal roofing bones (forming flanges and crests in some species), the presence of ornate sculptured patterns on the surfaces of dermal bones and in some species the appearance of a dermal sphenethmoid and additional dermal elements in the nasal region.

On the basis of the variation noted among hylids in the preceding discussion, it is evident that *Tripriion* and the other casque-headed hylids are highly specialized. The degree and nature of the morphological specialization can be assayed most efficiently by the comparison of *Tripriion* with the generalized and well-known *Smilisca baudini*. The genus *Smilisca* was treated systematically by Duellman and Trueb (1966), and the cranial morphology of *S. baudini* was described by Trueb (1968). In the following comparison of *S. baudini* with *Tripriion petasatus* emphasis has been placed on internal rather than the obvious external differences. The two species are referred to by their generic names throughout.

### The Olfactory Region

Anteriorly, the most obvious external difference between the two genera are the anterior position of the external nares and the presence of the prenasal in *Tripriion*. The premaxillary has rotated anteriorly, apparently in association with the prenasal. Thus the alary processes of the premaxillaries lie within the cavities of the prenasal, and the entire olfactory apparatus occupies a more anterior position than in *Smilisca*, in which the alary processes of the premaxillaries incline slightly posteriorly. The alary cartilage is shorter in *Tripriion* than in *Smilisca*. The alary cartilage is similarly located in both species, but in *Tripriion* the cartilage lies anterior to the solum nasi and thus does not fuse with the solum. The tectum nasi is much less extensive in *Tripriion* and does not form a roof to the cavum principale as it does in *Smilisca*.

The nasal cavities are similarly disposed with respect to one another in both species. However, the cavum principale is proportionately much larger in *Tripriion* than in *Smilisca*; in the former, the anterior end lies anterior to the premaxillary. The anterior end of the cavum medium occurs slightly anterior to the foramen for the ramus externus and medius narium in *Tripriion* and at the level of the foramen in *Smilisca*. The external nares are located in a more anterior position in *Tripriion*; the nares open into the cava principalae immediately posterior to the anterior end of the cava.

The superior prenasal cartilage is much longer in *Tripriion* than in *Smilisca*. The anterior end of the inferior prenasal cartilage lies at the base of the alary process of the premaxillary in both species, but in *Smilisca* the anterior end of the inferior prenasal cartilage lies at the level of the recessus medialis, whereas in *Tripriion* the anterior end of the cartilage lies posterior to this point. The inferior prenasal cartilage extends directly posterior to fuse with the solum nasi in *Tripriion*; in *Smilisca* it curves dorsally along the posterior surface of the alary process of the premaxillary before extending posteriorly to meet the solum. The inferior prenasal cartilage joins the solum nasi at the same level in both species.

The septomaxillaries of *Tripriion* and *Smilisca* are only slightly different. The medial and dorsal rami are more extensive in *Smilisca* than in *Tripriion*. In both species the ventral ramus is an anteroventral spur on the posterior end of the septomaxillary.

The crista subnasalis is situated farther posteriorly with respect to the nasal cavities in *Tripriion* than in *Smilisca*. Similarly, the anterior end of the anterior maxillary process lies more posterior in *Tripriion*. The plana terminalae of both species are similar. The planum antorbitale is much less extensive in *Tripriion* than in *Smilisca* and is not closely associated with the posterior end of the planum terminale as it is in *Smilisca*. Both species lack a processus lingularis.

### The Sphenethmoid and Orbital Regions

The sphenethmoid and orbital regions of *Tripriion* and *Smilisca* differ primarily in the degree of ossification, and in the presence of a dermally ossified sphenethmoid and greatly reduced palatine in *Tripriion*. Few differences obtain in the internal bones and cartilages of these regions. The bony medial septum of the sphenethmoid terminates posterior to the orbitonasal foramen in *Tripriion* and anterior to the orbitonasal foramen in *Smilisca*. The margin of the orbitonasal foramen is cartilaginous in *Smilisca* and bony in *Tripriion*. The entire sphenethmoid, except for a small part of the dorsolateral tip in the orbital region and the partly ossified taenia tecta marginalis, is bony in *Tripriion*, whereas the anterior and posterior parts of the sphenethmoid are cartilaginous in *Smilisca*. In both species the sphenethmoid diverges dorsomedially to produce a frontoparietal fontanelle. In *Tripriion* the fontanelle is obscured by the medial growth of the frontoparietals, whereas in *Smilisca* the fontanelle remains exposed, covered only by connective tissue, in which secondary calcification occurs in large adults.

### The Otic and Occipital Regions

The otic process is the most anterior otic structure in *Tripriion*; it lies at the posterior level of the optic foramen. The otic process almost immediately

merges with the pseudobasal process and then separates from it at the anterior level of the oculomotor foramen, where the otic process gives rise to the crista parotica dorsally. The cornu principalis of the hyale diverges ventrally at this level. By contrast, the most anterior otic structure in *Smilisca* is the anterior edge of the otic capsule, which lies at the anterior level of the oculomotor foramen. The anterior part of the pseudobasal process appears anterior to the otic process at the posterior level of the oculomotor foramen. The otic process merges immediately with the pseudobasal process and then diverges to form the crista parotica dorsally. The cornu principalis of the hyale does not diverge from the pseudobasal process until the level of the anterior acoustic foramen.

The anterior edge of the otic capsule lies at the anterior level of the prootic foramen in *Tripriion*. The crista parotica joins the medial edge of the otic capsule just posterior to this level. The crista joins the otic capsule at a corresponding level in *Smilisca*. At the posterior level of the prootic foramen, the pars externa plectri and pars ascendens plectri appear in *Tripriion*, whereas these do not appear in *Smilisca* until a level just anterior to the posterior acoustic foramen. The pars media plectri appears between the prootic and anterior acoustic foramina in *Tripriion* and between the anterior and posterior acoustic foramina in *Smilisca*. In both *Tripriion* and *Smilisca* the operculum appears at the level of the posterior acoustic foramen.

In *Tripriion* the otic region is heavily ossified; only the anterior part of the tectum synoticum, crista parotica, pars externa plectri, pars interna plectri, pars ascendens plectri, operculum, and ventrolateral ledge of the otic capsule are cartilaginous. By contrast, the otic region of *Smilisca* is largely unossified. The pars media plectri is ossified, as it is in *Tripriion*, but additional ossification is restricted to perichondral and endochondral ossification occurring in the sides of the neurocranium and the dorsum of the otic capsule, plus a small amount in the floor of the neurocranium. The remaining parts of the otic region are cartilaginous.

### The Bursa Angularis Oris

The bursa angularis oris is located in the same place in both *Tripriion* and *Smilisca*. However, the structure seems to be more highly organized in *Smilisca*; the bursa has a distinct central lumen, whereas in *Tripriion* the gland is represented only by a mass of unorganized lymphoid tissue.

### The Articular Region

The only obvious difference in the articular regions of the two genera is that the maxillary extensively overlaps the quadratojugal in *Tripriion*, whereas it only barely overlaps it in *Smilisca*.

### Discussion

The differences between the crania of *Smilisca* and *Tripriion* can be grouped into three categories: proportions; degrees of ossification of both endochondral and dermal elements; and the absence, reduction, or addition of elements.

The proportional differences are the most complex and difficult to interpret. The existence of a longer and more extensive olfactory

region in *Tripriion*, as compared with *Smilisca*, is suggested by the forward projection of the nasal cavities and cartilaginous structures anterior to the nasal cavities into the prenasal bone. The correspondingly identical positions of the posterior termini of the nasal cavities in both species precludes the idea that these structures merely have been shifted anteriorly in *Tripriion*; rather, the size of the nasal structures seems to have adjusted to correspond to the anterior position of the external nares and the anterior rotation of the premaxillary into the prenasal.

Like the olfactory region, the otic region extends over a proportionately greater distance in *Tripriion* than in *Smilisca*. The various cranial nerve foramina have been used as an index to the positions of the otic structures. This method, although not wholly satisfactory, is the most practical with the kinds of material and techniques available. The otic and pseudobasal processes and crista parotica project farther anteriorly in *Tripriion* than in *Smilisca*. The first of these elements appears at the posterior edge of the optic foramen. The anteriormost otic structure of *Smilisca* is the anterior edge of the otic capsule at the anterior level of the oculomotor foramen. This structure is followed by the pseudobasal and otic processes and crista parotica, respectively. The posteriormost otic structure, the operculum, appears at the level of the posterior acoustic foramen in both species. The posterior otic structures terminate at approximately the same level in *Tripriion* and *Smilisca*, whereas the anterior otic elements appear farther anteriorly in *Tripriion* than in *Smilisca*, and in the former the crista parotica and plectral apparatus are oriented anterolaterally. Perhaps these features in *Tripriion* are the result of internal adjustments to compensate for and balance the posterodorsal development of the heavy occipital crests.

Internal supportive structures tend to be reduced in *Tripriion*. The alary cartilage, tectum nasi, planum terminale, and planum antorbitale are much reduced in size in comparison with *Smilisca*. In *Tripriion* the palatine is present only as a vestige and the pterygoid does not brace the mandibular and suspensorial regions against the otic region of the cranium. These internal reductions contrast sharply with the addition of the prenasal and dermal sphenethmoid externally, and the otherwise extensive ossification in *Tripriion*, as compared with *Smilisca*. There is considerably less cartilage involved in the olfactory and otic regions of *Tripriion*. Many cartilaginous structures of *Tripriion* are reduced in size, and those which are not reduced, such as the nasal septum and solum nasi, are more

heavily ossified. Thus, in comparison with *Smilisca*, the skull of *Tripriion* is characterized by small cartilaginous elements and the absence of large blocks of cartilage.

By far the most striking contrast between *Tripriion* and *Smilisca* is the extensive ossification of external dermal bones in *Tripriion*, in which there is a proximal proliferation of bone so that the cranium is completely roofed. Furthermore, the paired dermal elements, such as the nasals and frontoparietals, converge on one another, and all dermal elements articulate with adjacent bones. In *Smilisca*, by comparison, only the posterior parts of the frontoparietels converge with one another, and the squamosal and frontoparietal are the only adjacent dermal elements which articulate with one another. *Tripriion* is characterized by distal proliferations of bone which result in wide spinose labial flanges, extensive supraorbital shelves, and exostosed bone over the entire surface of the skull. *Smilisca* lacks distal proliferation of bone, except for the small supra-orbital flange of the frontoparietal.

#### DEVELOPMENT OF THE OSTEOCRANIUM OF *Tripriion petasatus*

In the following description each bone is discussed separately. Membrane bones are treated first and are followed by cartilage bones. Bones are mentioned in the order of their appearance as accurately as this order could be ascertained from examination of available specimens. Four progressive stages of development of the skull are shown schematically in Figures 30 and 31. The stage in which cranial elements appear is depicted in Figure 33. Larval stages are those defined by Gosner (1960). Post-metamorphic stages represent successively more advanced specimens.

#### The Membrane Bones

*Frontoparietal*.—The frontoparietal first appears as a long rod of bone medial to the eye of the larva. There is no evidence of more than one center of ossification. Ossification spreads medially, anteriorly, and posteriorly from the initial center of growth. Bone proliferation seems to be most rapid in the posterior area where the paired frontoparietals first meet medially. The supraorbital flange develops along the lateral edge of the frontoparietal and appears between Post-metamorphic Stages 3 and 4, just prior to the advent of integumentary-cranial co-ossification of the frontoparietal.

*Nasal*.—The first center of ossification of the nasal is located dorsolaterally. The bone expands most rapidly anteriorly and ventrally; posteromedial and medial ossification progresses more slowly. Between Post-metamorphic Stages 3 and 4, the nasal develops a supraorbital process which expands posteriorly, lateral to the frontoparietal. At the same time integumentary-cranial co-ossification appears along the margin of the nasal bordering the orbit. Co-ossification

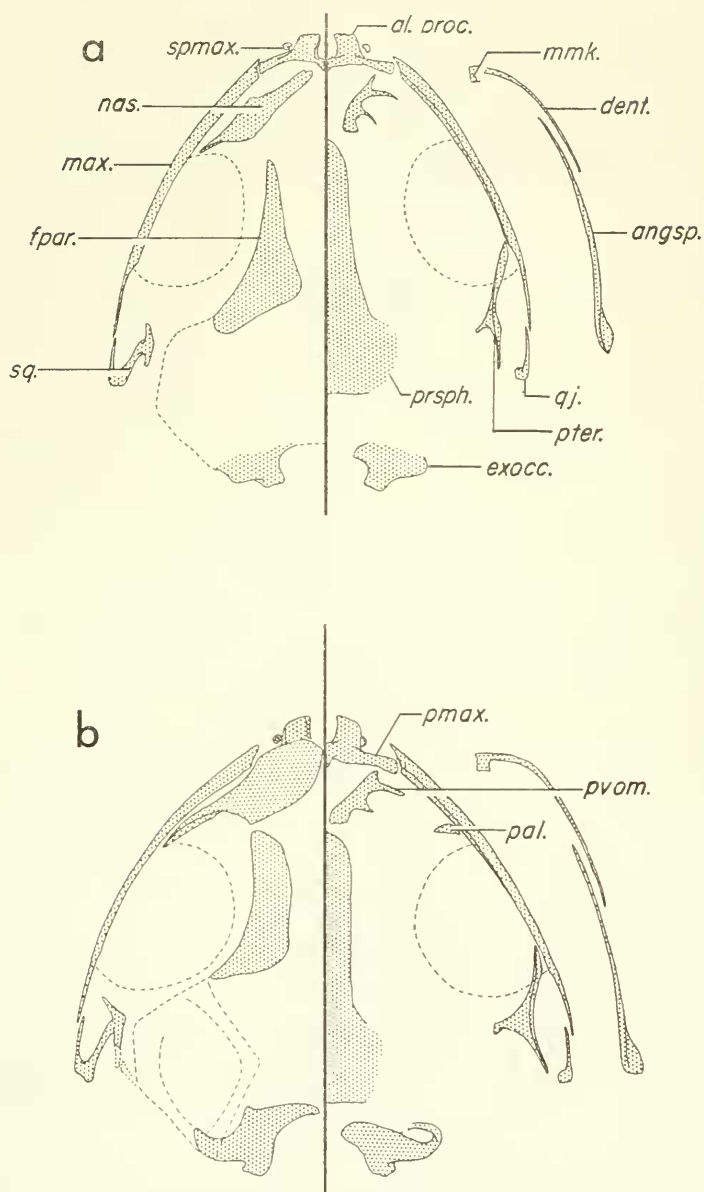


FIG. 30. Skulls of young *Triprion petasatus*. Dorsal and ventral views on right and left sides respectively of heavy median line. Right half of lower jaw shown to right of each skull. (a) recently metamorphosed young (KU 92639), snout-vent length 12.6 mm. approximately  $\times 20$ ; (b) young (KU 92638), snout-vent length 14.1 mm. approximately  $\times 18$ . Abbreviations: *al. proc.*, alary process of premaxillary; *angsp.*, angulosplenic; *col.*, columella; *dent.*, dentary; *exocc.*, exoccipital; *fpar.*, frontoparietal; *max.*, maxillary; *mmk.*, mentomeckelian; *nas.*, nasal; *pal.*, palatine; *pmax.*, premaxillary; *prsph.*, parasphenoid; *pter.*, pterygoid; *pvom.*, prevomer; *qj.*, quadratojugal; *spmax.*, septomaxillary; *sq.*, squamosal.

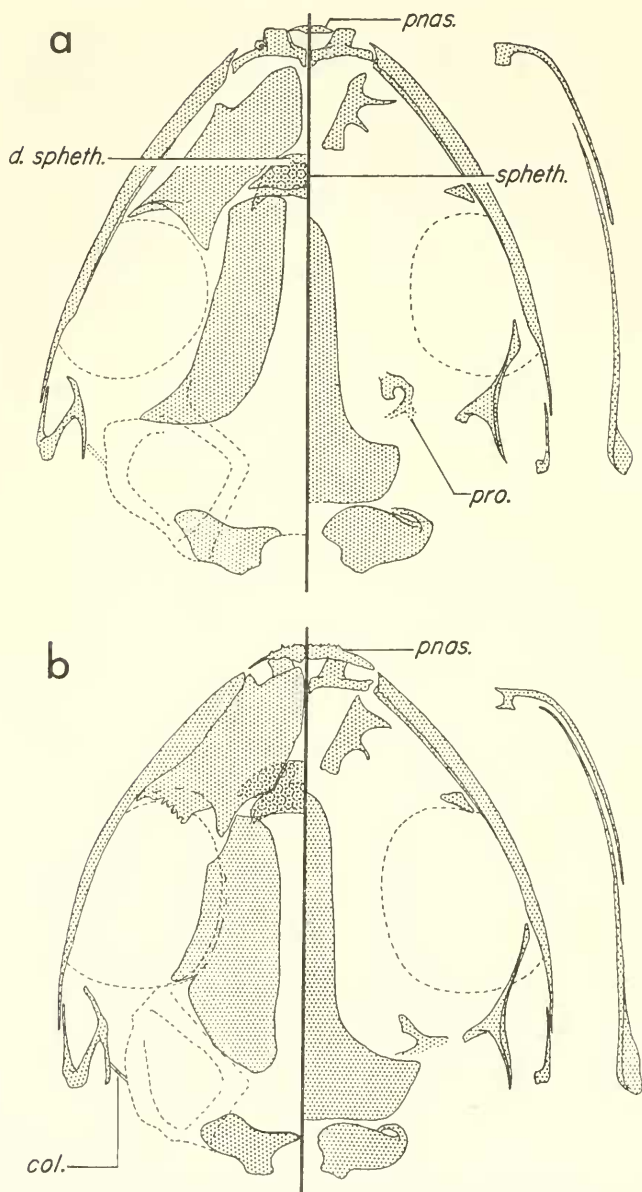


FIG. 31. Skulls of young *Tripurion petasatus*. Dorsal and ventral views on right and left sides respectively, of heavy median line. Right half of lower jaw shown to right of each skull. (a) young (KU 92637), snout-vent length of 15.5 mm. approximately  $\times 15$ ; (b) young (KU 92636), snout-vent length 17.5 mm. Abbreviations: *col.*, columella; *d. spheth.*, dermal sphenethmoid; *pnas.*, prenasal; *pro.*, prootic; *spheth.*, sphenethmoid. Refer to Fig. 30 for identification of other structures.

spreads over the entire surface of the nasal but proliferates most rapidly at the anterior edge of the orbit and in the canthal region. The accelerated growth of the former area gives rise to the serrate or spinose flange continuous with the supraorbital flange of the frontoparietal; these two elements, with the squamosal posteriorly, completely encase the eye of the adult frog. The rapid proliferation of bone in the canthal region results in the well-defined canthal ridge extending from the external nares and termination in the spinose preorbital knob of the mature specimen.

*Septomaxillary*.—The septomaxillary appears dorsally between the anterior end of the nasal and the alary process of the premaxillary. The bone is extremely small and is obscured from view early in development by growth of adjacent bones; thus, little is known about it.

*Premaxillary*.—The premaxillary appears early, as a small bone of the same form found in the adult. Besides over-all increase in size, two changes are noticeable. The first of these is the development of palatine processes on the posterior edge of the premaxillary. The second change, the more subtle and at the same time the more striking change, is the apparent forward rotation of the premaxillary. In early post-metamorphic specimens, the premaxillary lies in a position common to many anurans, wherein the alary process is slightly convex anteriorly and forms approximately a ninety-degree angle with the parietal plane of the skull. In subsequent post-metamorphic stages the premaxillary rotates so that the alary process projects anteriorly in association with the developing prenasal. In the adult frog the alary process lies within the prenasal. The premaxillary is not involved in integumentary–cranial co-ossification.

*Maxillary*.—Early changes in the maxillary involve the lengthening of the bone anteriorly and posteriorly. The bone extends forward, anterior to the level of the premaxillary, and posteriorly, to lie lateral to the developing quadratojugal. Soon after Post-metamorphic Stage 5 the maxillary fuses with the quadratojugal. Fusion commences at the posterior extremity of the maxillary and progresses anteriorly in the area of overlap between the maxillary and quadratojugal. A second early center of ossification lies in the anterior part of the maxillary and produces the pars facialis of the maxillary which articulates with the nasal dorsolaterally. Integumentary–cranial co-ossification appears after Post-metamorphic Stage 5 on the dorsum of the maxillary at the level of the articulation of the developing pterygoid and maxillary. Co-ossification progresses anteriorly, covering the pars facialis and the remaining dorsal surface. A rapid proliferation of bone along the dorsolateral margin of the maxillary results in the heavy, spinose maxillary flange characteristic of the adult frog.

*Squamosal*.—The ventral arm of the squamosal develops first. By Post-metamorphic Stage 1 it is attached to the quadratojugal ventrally. Subsequent areas of ossification are centered dorsally on the squamosal. The posterior arm increases in length first, followed by the anterior arm growing toward the maxillary anteroventrally. At the same time, bone proliferates dorsomedially so that the squamosal ultimately articulates with the frontoparietal dorsal to the prootic. Integumentary–cranial co-ossification commences in the latter region initially, and then spreads along the developing anterior arm.

*Parasphenoid*.—The parasphenoid appears early as a thin plate of ossification located centrally on the venter of the skull. Ossification seems to progress at an equal rate in all directions. The anterior end is completed first, followed by the lateral wings and the posterior part underlying the exoccipital and prootic. Apparently the odontoids develop at a late stage in the development of the skull.

*Pterygoid*.—The pterygoid develops rather slowly. Proximal parts of the bone appear first and the principal areas of early ossification involve the anterior and posterior rami; the medial ramus is the last part of the pterygoid to ossify, and never establishes contact with the prootic.

*Angulosplenic*.—The angulosplenic arises on the posteromedial part of Meckel's cartilage and grows both anteriorly and posteriorly. In later development the posterior parts of the angulosplenic and dentary fuse. The anterior part of the angulosplenic remains separated from the dentary and mentomeckelian by Meckel's cartilage.

*Dentary*.—The dentary appears anterior and lateral to Meckel's cartilage. A small proliferation of bone unites the dentary to the developing mentomeckelian. The greatest amount of ossification takes place posteriorly to lengthen the dentary and eventually unite it to the angulosplenic.

*Quadratojugal*.—The quadratojugal develops in association with the quadrate cartilage. It first appears around the cartilage and then ossifies anteriorly and extends along the medial surface of the maxillary for a short distance. The quadratojugal is not involved in integumentary–cranial co-ossification because the maxillary completely covers external parts of the bone.

*Palatine*.—Development of the palatine is foreshortened. It arises as a small sliver of bone oriented perpendicularly to the maxillary. Subsequent ossification widens the palatine in an anterior-posterior direction. The palatine remains very small and unattached to either the sphenethmoid or maxillary.

*Prevomer*.—The prevomer develops slowly. In early stages it consists of four radiating pieces of bone located medial to the internal nares. Later, the central part of the bone ossifies and extremities of the bone lengthen, so that in an adult specimen the prevomer is in contact with the premaxillary anteriorly and forms the anterior and part of the posterior margin of the internal nares. Prevomerine dentition does not appear until Post-metamorphic Stage 2, after the development of maxillary and premaxillary dentition.

*Prenasal*.—The rudimentary prenasal (Fig. 32a) is a small triangular piece of bone which lies anterior to the alary processes of the premaxillary. Proliferation of bone advances most rapidly in lateral areas (Fig. 32 b-e) and somewhat more slowly in a ventral direction. Integumentary–cranial co-ossification is well advanced by Post-metamorphic Stage 3 and is centrally located on the prenasal. Co-ossification advances rapidly to develop anteriorly projecting spines in a manner similar to that describing the development of the maxillary flange. However, growth of the prenasal relative to that of the maxillary flange is more prolonged and rapid. As the prenasal extends anteriorly, one must assume that a secondary resorption of the bone is taking place internally to form the internal prenasal cavities which accommodate the alary processes of the premaxillary as described for the adult frog. The ventral part of the prenasal is not involved in co-ossification. The prenasal expands until it is

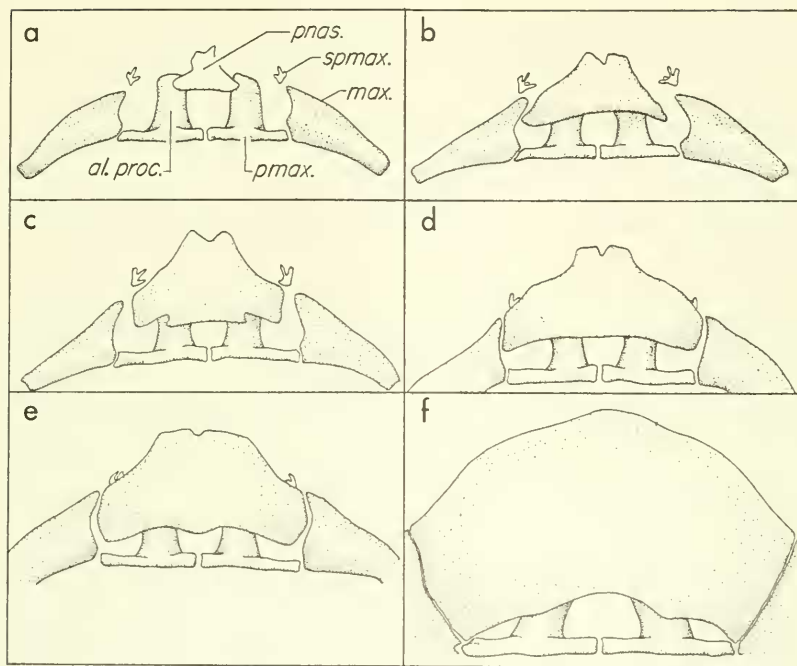


FIG. 32. Development of the prenasal bone in *Triprion petasatus*: (a) young (KU 92637), snout-vent length 15.5 mm.  $\times 13$ ; (b) young (KU 92635), snout-vent length 16.9 mm.  $\times 13$ ; (c) young (KU 92636), snout-vent length 17.5 mm.  $\times 13$ ; (d) young (KU 92634), snout-vent length 19.3 mm.  $\times 13$ ; (e) young (KU 92632), snout-vent length 20.3 mm.  $\times 13$ ; (f) young adult (KU 71744), snout-vent length 50.9 mm.  $\times 8$ . Abbreviations: *al. proc.*, alary process of premaxillary; *max.*, maxillary; *pmax.*, premaxillary; *pnas.*, prenasal; *spmax.*, septomaxillary.

narrowly separated from the premaxillary posteroventrally and in very close association with the maxillary laterally.

**Dermal Sphenethmoid.**—The dermal sphenethmoid is first visible as a delicate plate of ossification between the nasals and frontoparietals, overlying and discrete from the developing ossification of the endochondral sphenethmoid. The dermal sphenethmoid is initially ossified in the dense connective tissue layer of the lower dermis of the skin overlying the endochondral sphenethmoid. Subsequent ossification of the endochondral sphenethmoid unites it to the dermal sphenethmoid, and co-ossification of the latter results in the characteristically sculptured surface of the adult bone.

### The Cartilage Bones

**Exoccipital.**—The rudiment of the exoccipital probably appears between Larval Stages 43 and 45 since the exoccipital is well-formed by Post-metamorphic Stage 1. Subsequent bone proliferation closes the occipital arch and perichondral ossification appears in the basal plate and tectum synoticum. The exoccipital is not involved in integumentary-cranial co-ossification.

*Mentomeckelian*.—The mentomeckelian ossifies very early. The anterior part of the cartilage is replaced by bone initially and is fused with the adjacent dentary. Bone proliferation progresses posteriorly. The mentomeckelian remains separated from the angulosplenic by Meckel's cartilage.

*Columella*.—Bone first appears distally in the columella and ossification advances proximally.

*Prootic*.—The prootic is the last of the cranial bones to appear. It arises at the posterior border of the prootic foramen; ossification progresses over the otic capsule.

### COMPARATIVE DEVELOPMENT OF THE OSTEOCRANIUM

Comparison of the development of the osteocrania in anurans is difficult due to the lack of information about most species. The most comprehensive study on osteocranial development is that by Erdmann (1933) on *Rana temporaria*. Incomplete observations are available for *Eleutherodactylus nubicola* (Lynn, 1942), *Pseudacris triseriata triseriata* (Stokely and List, 1954), *Hyla septentrionalis* (Trueb, 1966) and *Smilisca baudini* (Duellman and Trueb, 1966). By contrast, there is a relative abundance of descriptive material available on the anuran chondrocranium (reviewed by de Beer, 1937).

The disproportionate amounts of information available on chondro- and osteocranial anuran development doubtlessly are a reflection of the difficulties encountered in post-metamorphic developmental studies. Anuran larvae are generally easily obtained and reared through desired developmental stages, whereas obtaining and rearing young frogs is appreciably more difficult. There are standardized larval stages whereby larvae can be categorized by degree of development without recourse to size or age. But once metamorphosis is reached there are no such criteria and thus no standards of comparison. Both size and age have been used as indices to post-metamorphic development. It has been shown previously (Trueb, 1966; and Duellman and Trueb, 1966) that size is an unreliable estimator of degree of development. Age, as utilized by Stokely and List (1954), is of value assuming one has a source of living specimens and adequate laboratory facilities.

Comparison of the appearance of cranial elements among *Smilisca baudini*, *Tripurion petasatus*, and *Hyla septentrionalis* is made in Figure 33. In view of the preceding discussion, it is obvious that the post-metamorphic stages designated in the figure are not strictly definable in precise terms as are the larval stages; in reality, the post-metamorphic stages simply represent conditions of progressive cranial development within each species. Thus there is only an approximate correlation between post-metamorphic stages of the different species. Consequently, the graph is most useful for observations on the sequence of bone development.

There seems to be little variation in the order of appearance of the cartilage bones. The exoccipital is the first cartilage-replacement bone to ossify; it appears in late larval stages in *Smilisca* and *Pseudacris* and in early post-metamorphic stages in *Tripurion* and *Hyla septentrionalis*. The exoccipital is followed by the mentomeckelian in each case; in *Tripurion* this bone appears at about the same time as the exoccipital, whereas in the other three genera it appears much later in post-metamorphic development, after most dermal elements have ossified. The columella, sphenethmoid, and prootic appear after the mento-

meckelian in rapid succession in *Triprion*. The sequence of ossification of these three structures is unknown in *Smilisca*. In *Hyla septentrionalis* the sphenethmoid and prootic precede the columella, whereas in *Pseudacris* the prootic precedes the sphenethmoid and columella.

The sequence of ossification of dermal bones is less well ordered and somewhat more complicated. In each of the four genera, the frontoparietal is among the first bones to appear during larval stages. In *Smilisca* the frontoparietal, septomaxillary and parasphenoid (all present in Larval Stage 40), are followed by the premaxillary, maxillary, dentary, squamosal, angulosplenial, and the maxillary and premaxillary dentition. These bones, as a group, are all present in Larval Stage 44. By contrast, only one to three dermal bones appear before metamorphosis in the other three genera. In *Triprion* the frontoparietal is followed by the nasal, which does not appear until early post-metamorphic stages in *Pseudacris*, *Smilisca*, and *Hyla septentrionalis*. In *H. septentrionalis* the frontoparietal and septomaxillary ossify during advanced larval stages and in *Pseudacris* the frontoparietal, premaxillary, and "nasal cartilage (calcification)" (? = septomaxillary) appear before metamorphosis.

There are few post-metamorphic cranial additions in *Smilisca*. The nasal, pterygoid, and prevomerine dentition are followed by ossification of the prevomer, quadratojugal, and palatine. This pattern contrasts sharply with the remaining three genera in which most dermal bones ossify during metamorphosis or early post-metamorphic stages. In *Triprion* all dermal bones and dentition except the prevomer, prevomerine dentition, dermal sphenethmoid, and prenasal appear during metamorphosis. Development is somewhat less rapid in *Hyla septentrionalis*. Most bones appear during metamorphosis except the palatine, and the quadratojugal and prevomerine dentition; the latter structures ossify subsequent to the appearance of the palatine. The pattern is similar in *Pseudacris*; however, the majority of bones appearing early are followed by the quadratojugal first and then the palatine and parasphenoid.

Some interesting deviations in the sequence of ossification exist among dermal bones of these four genera. The prevomer appears during or shortly after metamorphosis in all genera except *Smilisca* in which it is one of the last bones to ossify. The prevomer and prevomerine dentition appear at the same time in *Triprion*. In *Smilisca* prevomerine dentition appears before complete ossification of the bone, and by contrast the prevomer is well ossified in *Hyla septentrionalis* before the appearance of its dentition. The parasphenoid is among the earliest bones to ossify in *Smilisca*, *Triprion*, and *Hyla septentrionalis*, but in *Pseudacris* it is one of the last. The quadratojugal appears late in development in all genera except *Triprion*.

The sequences of ossification in these four genera compare favorably with the pattern described for *Rana temporaria* with two exceptions. The prootic appears before the mentomeckelian, and the nasal appears quite later in development of *Rana*. The pattern of development of *Rana* more closely resembles that of *Pseudacris*, *Triprion*, and *Hyla septentrionalis* than *Smilisca*, in that only the parasphenoid, frontoparietal, premaxillary, and exoccipital appear before metamorphosis. The meager data available for *Eleutherodactylus nubicola* suggest that it is quite different from the preceding genera discussed. If hatching in *Eleutherodactylus* is considered to be more or less equivalent to metamorphosis in other anurans, then *E. nubicola* is similar to *Smilisca* in the

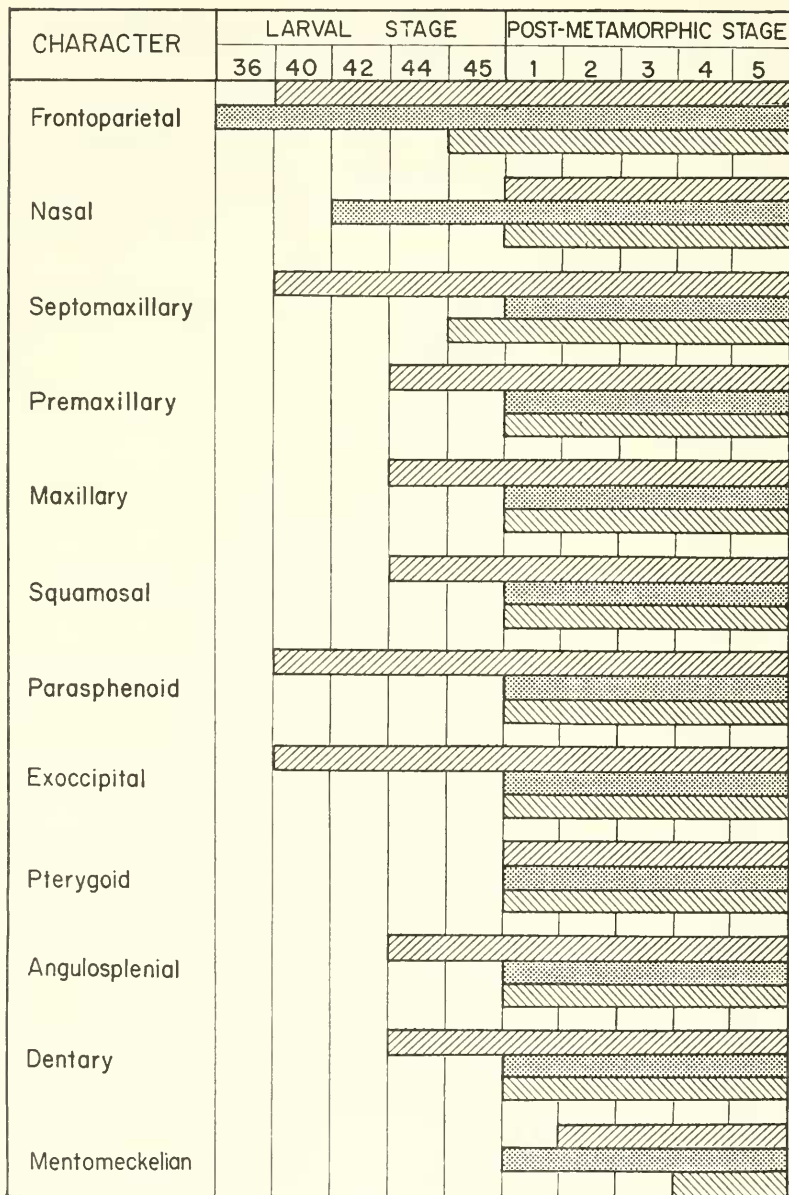


FIG. 33, first segment. The order of occurrence of cranial ossifications in the skulls of three hylid frogs. In each group of three bars, the uppermost bar (cross-hatching) represents *Smilisca baudini*, the middle bar (dots), *Tripriorion petasatus*, and the lower bar (cross-hatching), *Hyla septentrionalis*.

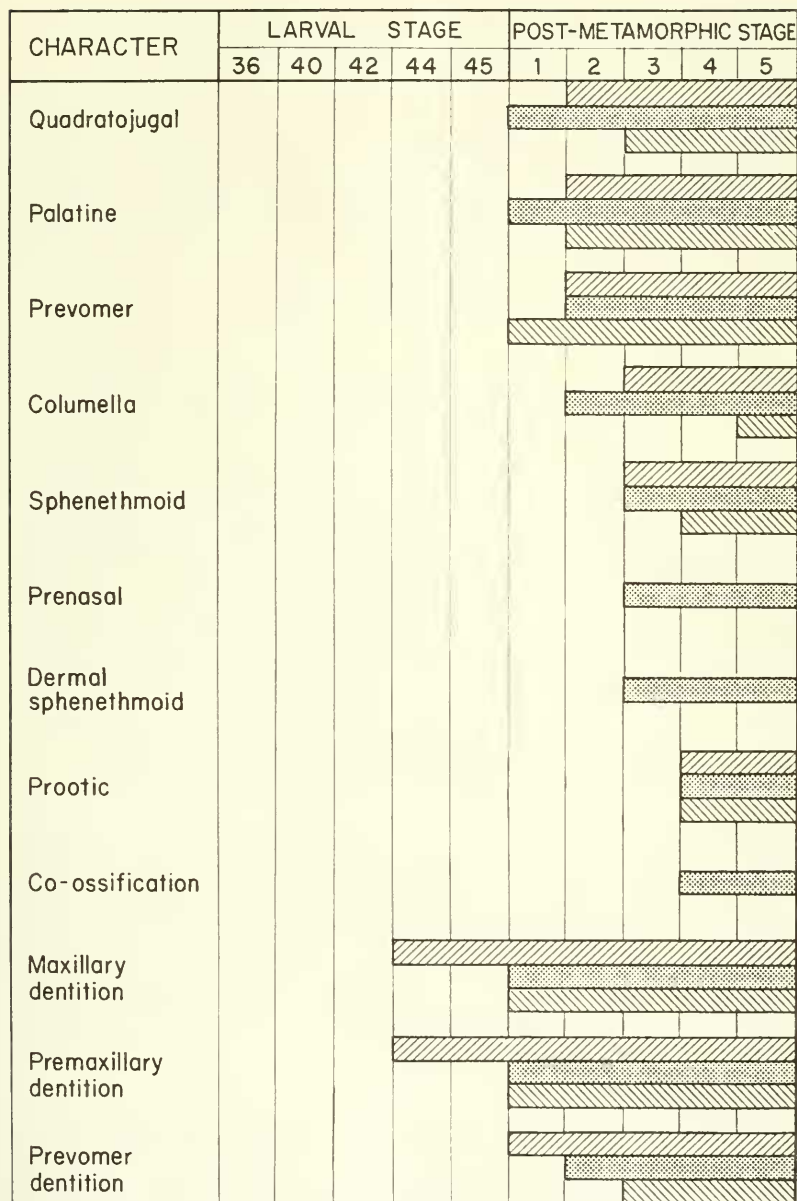


FIG. 33, second segment. Legend on facing page.

early larval development of dermal bones. However, it differs from *Smilisca* in the appearance of the angulosplenial, squamosal, and parasphenoid before the premaxillary, dentary, and frontoparietal, respectively.

Obviously, there is a great deal more flexibility in the development of dermal cranial elements as compared with cartilage bones. Moreover, it is interesting to note that the dermal elements which appear the latest in development in the hylid genera discussed are those structures which are most often reduced or absent among hylids. For example, the pterygoid often lacks bony articulations with the articular region posteriorly and the prootic medially. I know of no case in which the prevomer has been lost, but it is not unusual for the bone to lack teeth. The palatine is reduced in some frogs, notably in *Triprrion*. The quadratojugal is probably the most common cranial structure to be reduced or totally lost among hylids.

As one would expect, addition of the dermal sphenethmoid to the crania of *Hyla septentrionalis* and *Triprrion* occurs following the initial ossification of all other dermal bones. The prenasal appears in *Triprrion* with the dermal sphenethmoid. Subsequent to the development of all dermal bones, integumentary-cranial co-ossification commences on their surfaces. The development of co-ossification generally corresponds to original centers of ossification and follows the pattern of proliferation of dermal bone. The process of co-ossification is the same in *Triprrion* as it is in *Hyla septentrionalis*, which has been described by Trueb (1966). Co-ossification starts relatively earlier in *Triprrion* than in *H. septentrionalis*, and co-ossification together with the expansive distal proliferation of dermal bones creates the highly contoured skull characteristic of *Triprrion*. This sequence of events suggests that the bizarre cranial modifications of *Triprrion*, and probably the other casque-headed hylids, are evolutionarily recent specializations, rather than primitive characters.

#### THE OCCURRENCE OF THE CASQUE-HEADED CO-OSSIFIED CRANIUM WITHIN THE FAMILY HYLIDAE

The occurrence of integumentary-cranial co-ossification and/or the development of a casque is widespread in the family Hylidae. One or both conditions are characteristic of the following genera: *Amphignathodon*, *Anotheca*, *Aparasphenodon*, *Corythomantis*, *Diaglena*, *Hemiphractus*, *Nyctimantis*, *Osteocephalus*, *Pternohyla*, *Tetraprrion*, *Trachycephalus*, and *Triprrion*. Also included are some species of *Hyla* (*brunnea*, *dominicensis*, *fimbrimembra*, *lichenata*, *miliaria*, and *septentrionalis*) and *Gastrotheca* (*weinlandi*, *fulvorufa*, *nicefori*, and *ovifera*).

Members of the genus *Hemiphractus* are characterized by extremely bizarre skulls which are heavily casqued. The skin of the skull is not co-ossified with the underlying bone; thus, the osteology of this group is not pertinent to the problem at hand. In fact, the cranium of *Hemiphractus* is unlike that of any other hylid; perhaps further study will show that the frogs in this genus represent an early phyletic divergence from other hylids.

The skulls of two species of fringe-limbed hylids (*Hyla fimbriembra* and *H. miliaria*) seem to be co-ossified in preserved specimens. Examination of a skull of *Hyla miliaria* reveals that the cranium of this species is not co-ossified. Radiographs of *Hyla fimbriembra* show the presence of numerous osteoderms; these are characteristic of adults of both *H. miliaria* and *H. fimbriembra*. Their presence renders the skin of the cranium immovable and thus simulates the co-ossified condition. It is probable that osteoderms represent one of the first adaptive steps in the evolution of a co-ossified cranium. The fringe-limbed hylids are represented by so few specimens that sufficient material is not available to pursue studies of the cranium.

*Anotheca*, *Nyctimantis*, and *Amphignathodon*, *Gastrotheca*, and possibly *Flectonotus* seem to form a natural group of genera within the Hylidae. This group displays similarity in the external morphology of its members, their life histories, and their tendency towards arboreal habits. The skulls are casqued and co-ossified in all of these frogs, except some species of *Gastrotheca*. It is possible that these comprise a group in which the casque-headed, co-ossified condition has been derived independently. However, specimens necessary to the evolution of this hypothesis were not available to the present study. The remaining genera of casque-headed, co-ossified hylids are treated in this paper.

My studies on the cranial morphology provided evidence which necessitates certain modifications in the existing generic classification of the casque-headed, co-ossified hylids. In the following account of cranial osteology, data are presented which support the generic synopsis given below. The genera are listed alphabetically, and generic synonyms are given chronologically. In the lists of included species, synonyms are given in brackets.

### Synopsis of the Genera

#### *Aparasphenodon* Miranda-Ribeiro

*Aparasphenodon* Miranda-Ribeiro, 1920:86 [Type species, *Aparasphenodon brunoi* Miranda-Ribeiro, 1920:87, by monotypy].

*Diagnosis*.—Skull longer than broad; snout, in dorsal view, narrow, acuminate; canthal ridges distinct, anteriorly concave; surface configuration of dermal roofing bones consisting of reticulate network of ridges in low relief and prominent patterns of radial ridges; prenasal present; alary processes of premaxillaries concealed by prenasal, anteriorly inclined; internasal absent; palatines present; dermal sphenethmoid present; vocal sac single, median, subgular.

*Range*.—Coastal region of southeastern Brazil and (?) upper Orinoco Basin of Venezuela.

*Included Species*.—*A. brunoi* Miranda-Ribeiro, 1920 [*Corythomantis adspersa* Lutz, 1926; *Corythomantis apicalis* Miranda-Ribeiro, 1920], (?) *Corythomantis venezolana* Mertens, 1950.

*Remarks*.—Carvalho (1941) pointed out that *Corythomantis adspersa* and *C. apicalis* are names based on juveniles of *Aparasphenodon brunoi*. Mertens (1950) named *Corythomantis venezolana* from San Fernando de Atabapo, Venezuela. I have examined photographs and radiographs of the unique holotype. Although it is not possible to discern the exact nature of the cranial elements from radiographs, a prenasal bone and palatines seem to be present (both absent in *Corythomantis*). The canthal ridges are distinct (indistinct in *Corythomantis*) and anteriorly concave. Furthermore, the shape of the snout and the configuration of the dermal roofing bones are reminiscent of those of *Aparasphenodon brunoi*.

### *Corythomantis* Boulenger

*Corythomantis* Boulenger, 1896:405 [Type species, *Corythomantis greeningi* Boulenger, 1896:405, by monotypy].

*Diagnosis*.—Skull longer than broad; snout in dorsal view moderately narrow but rounded; canthal ridges indistinct; surface configuration of dermal roofing bones consisting of reticulate network of ridges in low relief; prenasal absent; alary processes of premaxillaries concealed by nasals, anteriorly inclined; internasal absent; palatines absent; dermal sphenethmoid present; vocal sac single, median, subgular.

*Range*.—Xeric region of northeastern Brazil.

*Included Species*.—*C. greeningi* Boulenger, 1896 [*C. schubarti*, Miranda-Ribeiro, 1937].

*Remarks*.—Carvalho (1941) placed *C. schubarti* in the synonymy of *C. greeningi*.

### *Osteocephalus* Steindachner

*Osteocephalus* Steindachner, 1862:77 [Type species, *Osteocephalus taurinus* Steindachner, 1862:77, by original designation (not *Osteocephalus taurinus* Fitzinger, 1843:50 a *nomen nudum*)].

*Diagnosis*.—Skull broader than long; snout in dorsal view broad, truncate; canthal ridges distinct, not anteriorly concave; surface configuration of dermal roofing bones consisting of poorly-developed ridges; prenasal absent; alary processes of premaxillaries exposed, not co-ossified, not anteriorly inclined; internasal absent; palatines present; dermal sphenethmoid present, poorly developed; vocal sacs paired, lateral, behind angles of jaws.

*Range*.—Amazon Basin.

*Included Species*.—*O. lepieuri* (Duméril and Bibron, 1841) [*O. planiceps* Cope, 1874]; *O. taurinus* Steindachner, 1862 [*O. flavolineatus* Steindachner, 1862].

*Remarks*.—Goin (1961) noted that eight or ten species probably are included in this genus. Until they have been adequately studied, I hesitate to include any species in the genus other than those that I have examined.

### *Pterohyla* Boulenger

*Pterohyla* Boulenger, 1882:326 [Type species, *Pterohyla fodiens* Boulenger, 1882:326, by monotypy].

**Diagnosis.**—Skull broader than long; snout in dorsal view broadly rounded; canthal ridges indistinct; surface configuration of dermal roofing bones consisting of network of prominent bony spines; prenasal absent; alary processes of premaxillaries exposed, co-ossified or not, not anteriorly inclined; internasal present (*P. fodiens*) or absent (*P. dentata*); palatines present; dermal sphenethmoid absent; vocal sac bilobed, subgular.

**Range.**—Extreme southwestern Arizona in the United States, southward at low and moderate elevations to Michoacán, México.

**Included Species.**—*P. dentata* Smith, 1957; *P. fodiens* Boulenger, 1882 [*Hyla rudis* Mocquard, 1899].

**Remarks.**—Kellogg (1932) showed that the type of *Hyla rudis* Mocquard is a juvenile of *Pterohyla fodiens*.

### *Trachycephalus* Tschudi

*Trachycephalus* Tschudi, 1838:74 [Type species, *Trachycephalus nigromaculatus* Tschudi, 1838:74, by monotypy].

*Tetraprion* Stejneger and Test, 1891:167 [Type species, *Tetraprion jordani* Stejneger and Test, 1891:167, by original designation].

**Diagnosis.**—Skull as long as broad or slightly longer than broad; snout in dorsal view rounded with medial notch; canthal ridges distinct, not anteriorly concave; surface configuration and dermal roofing bones consisting of reticulate network of ridges and patterns of radial ridges in moderate relief; prenasal absent; alary processes of premaxillaries exposed, expanded, co-ossified, not anteriorly inclined; internasal absent; palatines present; dermal sphenethmoid present; vocal sacs paired, lateral, behind angles of jaws.

**Range.**—Northeastern Brazil southward to eastern Argentina in the La Plata Delta; Pacific slopes of Colombia and Ecuador.

**Included Species.**—*T. atlas* Bokermann, 1966; *T. jordani* (Stejneger and Test, 1891); *T. nigromaculatus* Tschudi, 1838 [*T. geographicus* Duméril and Bibron, 1841; *T. marmoratus* Steindachner, 1864; *T. occipitalis* Fitzinger, 1864; *Hyla angustifrons* Werner, 1893]; *T. siemersi* (Mertens, 1937).

**Remarks.**—In the original description of *Tetraprion jordani* Stejneger and Test (1891:168) assigned the frog generic status because “. . . it differs from all known *Hylidae* in possessing teeth on the palatines.” Subsequent authors (Rivero, 1961; Peters, 1955; Smith, 1957; and Myers, 1942) discussed the generic relationships but unaccountably overlooked the striking resemblance of *Tetraprion* to *Trachycephalus nigromaculatus* Tschudi, 1838. Both frogs have palatine odontoids; those of *Trachycephalus* are better developed than those of *Tetraprion*. *Trachycephalus* lacks parasphenoid odontoids, but bears a prominent ventral ridge on the parasphenoid. The basic structure of the skulls of both genera is nearly identical. In both frogs the medial rami of the pterygoids fail to articulate with the prootics, and the squamosal arches are incomplete. The

alary processes of the premaxillaries are expanded and co-ossified. Because the processes do not fuse medially, there appears to be a medial premaxillary "notch." The general appearance of the dorsal aspects of the skulls is similar. *Tetraprion* has carried the process of co-ossification and expansion of dermal bones somewhat further than *Trachycephalus*; thus the maxillaries and premaxillaries are more extensive and heavily sculptured, and the frontoparietals terminate posteriorly in a moderate, upturned occipital crest. Both frogs share the unusual character of having paired, lateral vocal sacs located behind the angles of the jaws. In view of the foregoing evidence it seems only reasonable to place *Tetraprion* in the generic synonymy of *Trachycephalus*.

### Tripriion Cope

*Pharyngodon* Cope, 1865:193 [Type species, *Pharyngodon petasatus* Cope, 1865:193, by monotypy; preoccupied by *Pharyngodon* Diesing, 1860 (Nematelminthes)].

*Tripriion* Cope, 1866:127 [Substitute name for *Pharyngodon* Cope, 1865, preoccupied].

*Diaglena* Cope, 1887:12 [Type species, *Tripriion spatulatus* Günther, 1882:279, by original designation].

*Diagnosis*.—Skull longer than broad; snout in dorsal view moderately acuminate; canthal ridges distinct anteriorly concave; surface configuration of dermal roofing bones consisting of extremely fine reticulate network of ridges and patterns of radial ridges; prenasal present; alary processes of premaxillaries concealed by prenasal, anteriorly inclined; internasal absent; palatines present, reduced; dermal sphenethmoid present (*T. petasatus*) or absent (*T. spatulatus*); vocal sac bilobed (*T. petasatus*) or single (*T. spatulatus*), subgular.

*Range*.—Disjunct; Pacific lowlands from Sinaloa to Oaxaca, México; Yucatan Peninsula of México, and northern Guatemala.

*Included Species*.—*T. petasatus* Cope, 1865; *T. spatulatus* Günther, 1882 [*Diaglena reticulata* Taylor, 1942].

*Remarks*.—Cope (1887:12) proposed the generic name *Diaglena* for *Tripriion spatulatus* Günther, 1882, and diagnosed *Diaglena* as differing from *Tripriion* (*T. petasatus* sole included species) ". . . in having a transverse instead of vertical pupil." Taylor (1942) named *Diaglena reticulata*, but Duellman (1968) provided evidence that *D. reticulata* and *D. spatulata* are conspecific. The skulls of *Tripriion* and *Diaglena* are very similar in general appearance. The skull of *Tripriion* is more depressed centrally than is that of *Diaglena*; the canthal ridges terminate posterior to the external nares, whereas they terminate anterior to the external nares in *Diaglena*; the prenasal is dorsally concave in *Tripriion* and nearly flat in *Diaglena* and *Tripriion* has a dermal sphenethmoid which is absent in *Diaglena*. In all other respects, both internal and external, the skulls of the two genera are nearly identical. Duellman and Klaas (1964) demonstrated that the pupil of *Tripriion petasatus* is horizontally elliptical. In view of the latter information, and the morphological similarities of the two frogs, *Diaglena* should be a generic synonym of *Tripriion*. The geographic complementarity of their ranges is in agreement with this conclusion.

Cranial Morphology of *Hyla septentrionalis*

The skull of *Hyla septentrionalis* is broader than long (Pl. 4a, b); the snout in dorsal view is slightly truncate. The dermal roofing bones are moderately to heavily casqued and partly co-ossified. The dorsal surfaces of the dermal bones are rugose and in some places fused with the overlying skin. *Hyla septentrionalis* lacks a prenasal and internasal. There are no labial flanges nor is there an occipital crest. A dermal sphenethmoid is present. The frontoparietals bear a broad supraorbital flange which is not conspicuously upturned; the frontoparietal usually does not cover the entire crista parotica posterolaterally. The prevomerine teeth are straight (see Table 1) or slightly curved (see Table 1). The anterior arm of the squamosal usually does not articulate with the maxillary. The vocal sac is single, median and subgular. The external morphology of the skull of *Hyla septentrionalis* has been described (Trueb, 1966); the following account is concerned only with the internal cranial anatomy.

*The Olfactory Region.*—The anterior end of the septum nasi appears between the alary processes of the premaxillaries (Fig. 34). The inferior prenasal cartilage lies along the posterior surface of the alary process of the premaxillary (Fig. 34). The superior prenasal cartilage is massive and closely associated with the alary cartilage. The anterior end of the superior prenasal cartilage lies adjacent to the posterodorsal tip of the alary process of the premaxillary and is posterolaterally connected to the alary cartilage. At successive levels posterior to the level of the premaxillary, the solum nasi appears, the foramina for the ramus externus narius and ramus medius narius enter the solum, the alary cartilage fuses with the septum nasi, and the anterior end of the cavum medium appears. The anterior end of the cavum inferius lies posteroventral to the cavum medium and anterior to the anterior level of the cavum principale (Fig. 35). The inferior prenasal cartilage fuses with the solum nasi at the level of the anterior margin of the external naris. The tectum nasi is well developed and a crista subnasalis is present. The first ossification of the nasal region is perichondral ossification of the septum nasi at the mid-level of the olfactory eminence. In posterior sections, the ventral part of the solum ossifies first. At the level of the anterior margin of the internal naris, the dorsal part of the septum begins to ossify. The septum and solum nasi are completely ossified anterior to the posterior margins of the internal nares, and are synosteotically united with the sphenethmoid posteriorly.

The anterior end of the septomaxillary is broad and thin and lies dorsolateral to the cavum medium (Fig. 36). The septomaxillary expands ventrolaterally around the lateral end of the cavum medium. The ventrolateral flange of the septomaxillary bifurcates from the broad anterior ramus and expands posteromedially ventral to the cavum medium. In subsequent sections, the anterodorsal ramus of the septomaxillary thickens and then bifurcates into a medial ramus associated with the lamina superior and a lateral ramus. Posterior to the bifurcation, the medial ramus diminishes in size, whereas the lateral ramus develops a high dorsal crest and fuses with the ventral ramus posterior to the divergence of the nasolacrimal duct from the cavum medium.

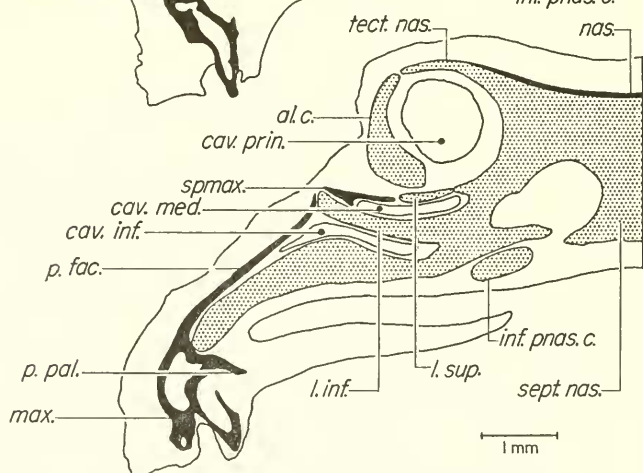
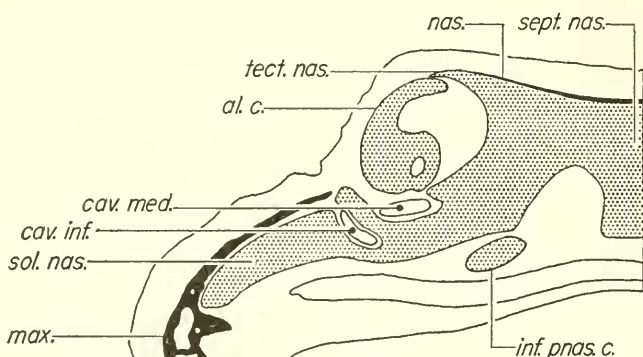
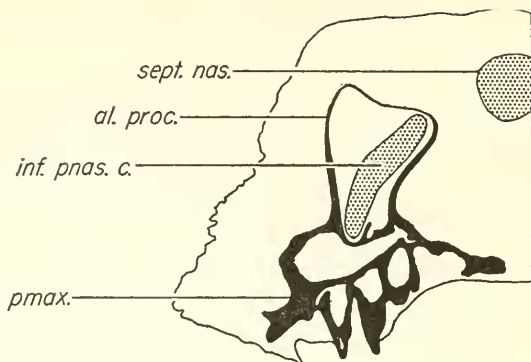
*The Sphenethmoid and Orbital Region.*—The sphenethmoid is in synosteotic continuity with the septum nasi anteriorly. At the level of the orbitonasal foramen (Fig. 37), the sphenethmoid is entirely bony except for the distal tip of

TABLE 1.—Geographical and Morphological Characters of Casque-headed, Co-ossified Hyliids and Related Forms. Symbols and Abbreviations: (—), absent; (+), present; (//), not concave anteriorly; ( ), concave anteriorly; (R), reduced; (I) Type I septomaxillary; (II) Type II septomaxillary; exp., expanded; mod., moderate.

SPECIES	DISTRIBUTION	Vocal Sac	Internasal	Prenasal	Dermal sphenethmoid	Prevomarine teeth	Palatine	Septomaxillary	Bifurcate cavum principale	Anterior acoustic foramen	Posterior acoustic foramen	Quadratrigonal	Labial flange	Canthal ridges
<i>Hyla septentrionalis</i>	Cuba, Bahamas, Isle of Pines, Florida.	single, median.	—	—	+	)	+	II	—	+	+	+	—	/
<i>Hyla brunnea</i>	Jamaica	single, median.	—	—	+	)	+	(?)	—	+	+	+	—	/
<i>Hyla dominicensis</i>	Hispaniola	single, median.	—	—	+	)	+	(?)	—	+	+	+	—	/
<i>Phrynohyas venulosa</i>	Pacific and Atlantic lowlands of México to Argentina.	paired, lateral.	—	—	—	)	+	II	—	+	+	+	—	—
<i>Osteocephalus taurinus</i>	Wet forests of interior and northern South America.	paired, lateral.	—	—	+	∧	+	II	—	+	+	+	—	/
<i>Trachycephalus nigromaculatus</i>	Southeastern Brazil.	paired, lateral.	—	—	+	)	+	II	—	+	+	+	mod.	/
<i>Trachycephalus atlas</i>	Bahia, Brazil.	paired, lateral.	—	—	+	)	+	(?)	—	+	+	+	mod.	/
<i>Trachycephalus jordani</i>	Pacific slopes of Colombia and Ecuador.	paired, lateral.	—	—	+	)	+	II	—	+	+	+	mod.	/

TABLE 1.—*Concluded*

SPECIES	DISTRIBUTION	Vocal Sac	Internasal	Prenasal	Dermal sphenethmoid	Prevomerine teeth	Palatine	Septomaxillary	Bifurcate cavum principale	Anterior acoustic foramen	Posterior acoustic foramen	Quadratrigonal	Labial flange	Canthal ridges
<i>Corythomantis greeningi</i>	Cadanga of Brazil.	single, median.	—	—	+	∧	—	II	—	+	+	R	mod.	—
<i>Aparasphenodon bruni</i>	Restinga of south-eastern Brazil.	single, median.	—	+	+	∧	R	II	—	+	—	R	mod.	/
<i>Triprion spatulatus</i>	Lowlands of western México.	single, median.	—	+	—	∧	R	I	+	+	+	+	exp.	/
<i>Triprion peltatus</i>	Yucatan Peninsula and northern Guatemala.	single, bilobed.	—	+	+	∧	R	I	+	+	+	+	exp.	/
<i>Pternohyla dentata</i>	Lowlands and moderate elevations of western México.	single, bilobed.	+	—	—	∧	+	I	+	+	+	+	mod.	—
<i>Pternohyla fodiens</i>	Río Santiago Basin of Mexican Plateau.	single, bilobed.	+	—	—	∧	+	I	+	+	—	+	mod.	—
<i>Smilisca baudini</i>	Pacific and Atlantic lowlands of México to Costa Rica.	single, bilobed.	—	—	—	—	+	I	+	+	+	+	—	—



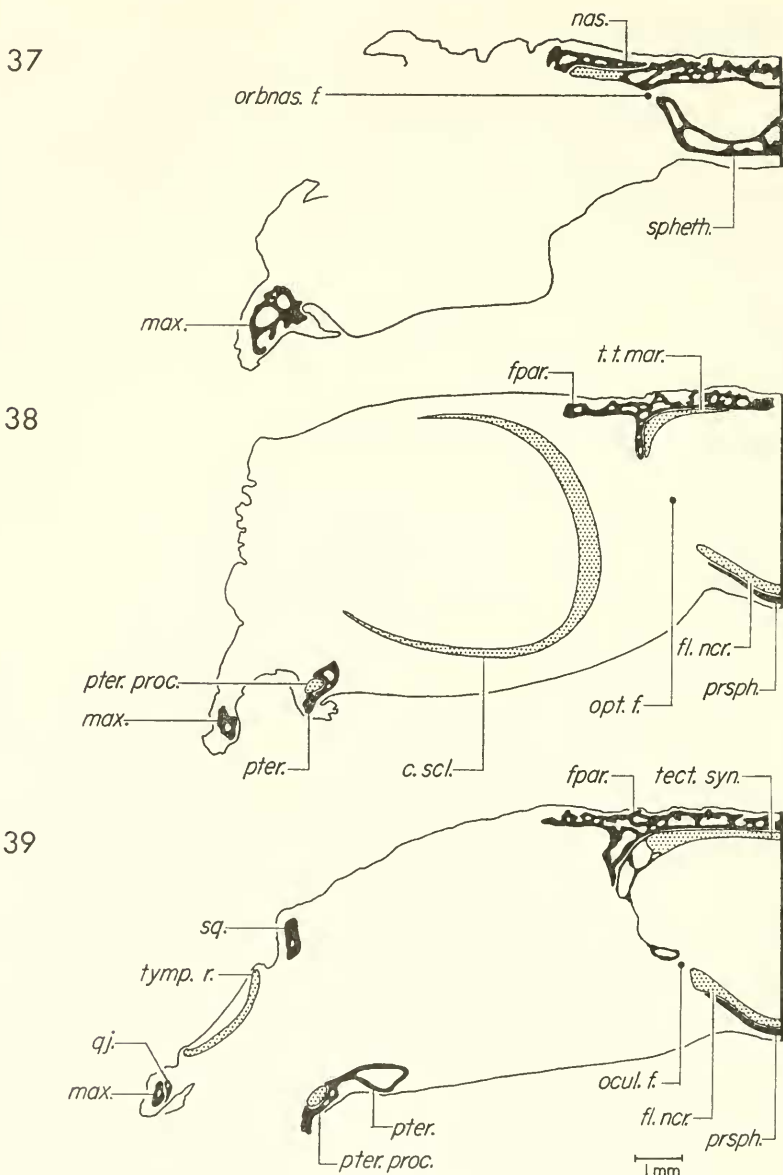
FIGS. 34-36. Transverse sections through the anterior end of the skull of *Hyla septentrionalis* (KU 89930): (34) level of alary process of premaxillary; (35) anterior level of cavum medium; (36) anterior levels of cavum principale and septomaxillary. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *cav. inf.*, cavum inferius; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *p. fac.*, pars facialis of maxillary; *p. pal.*, pars palatina of maxillary; *pmax.*, premaxillary; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary; *tect. nas.*, tectum nasi.

the anterolateral wing, which is cartilaginous. In posterior sections, the cartilage expands into a broad supraorbital shelf which is detached from the bony parts of the sphenethmoid in the mid-part of the orbit. Posterior to the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. Anteriorly, the margins of the fontanelle are bony. Cartilage appears laterally in the sphenethmoid in the posterior part of the orbit. In subsequent sections, bone disappears dorso-laterally and cartilage appears at the margins of the optic foramen. A short distance anterior to and at the level of, the optic foramen, the sphenethmoid is completely cartilaginous.

The bursa angularis oris is moderately well developed. It lies between the pterygoid and maxillary in the posterior part of the orbit. The anterior end of the bursa is a mass of lymphoid tissue, which is loosely encapsulated in connective tissue. A short, central lumen of small diameter precedes the simple, longitudinal aperture connecting the gland with the oral cavity; another small, central lumen appears near the end of the bursa.

*The Otic and Occipital Regions.*—The posterior margins of the optic foramen (Fig. 38) are formed in bone by the perichondral and dorsolateral endochondral ossification of the prootic, and the lamina perpendicularis of the frontoparietal. The trochlear nerve utilizes the optic foramen but is separated dorsally from the optic nerve by connective tissue. The oculomotor foramen (Fig. 39) lies just posterior and ventral to the optic foramen. The dorsal margin of the oculomotor foramen is bony, whereas the anteroventral edge is cartilaginous; posteroventrally, the margin is ossified. A thick bridge of bone separates the oculomotor foramen from the more posterior prootic foramen (Fig. 40). The margins of the prootic foramen are bony. Posteriorly, the anterior acoustic foramen (Fig. 41) lies in bone anteriorly and posteroventrally, and in cartilage posterodorsally. The anterior acoustic foramen is narrowly separated by cartilage and bone (perichondral ossification) from the posterior acoustic foramen (Fig. 42). The posterior acoustic foramen is bordered by bone on all but the anterior margin. The jugular foramen lies in bone a short distance posterior to the posterior acoustic foramen.

The most anterior part of the otic region is the pseudobasal process, the anterior end of which lies at the posterior level of the oculomotor foramen. In posterior sections, the pseudobasal process enlarges and expands medially (Fig. 40). At the anterior level of the prootic foramen, the otic process lies medially adjacent to the squamosal dorsolaterally. The otic process extends postero-ventrally, and fuses with the dorsolateral corner of the pseudobasal process. Posteriorly, the otic process loses its connection with the pseudobasal process and expands medially to fuse with the otic capsule and form the crista parotica (Fig. 41). The pseudobasal process fuses medially with the otic capsule at the posterior margin of the prootic foramen. Just posterior to the latter level, the cornu principalis of the hyale diverges posteroventrally from the ventro-lateral edge of the otic capsule. The pars externa plectri lies at the level of the anterior acoustic foramen. A short distance posterior the medial part of the pars media plectri appears, and is followed by the pars interna plectri (Fig. 42). The pars ascendens plectri and the distal part of the pars media plectri lie at the posterior margin of the anterior acoustic foramen. The mid-part of the pars media plectri and the posterior end of the pars externa plectri lie im-



FIGS. 37-39. Transverse sections through the skull of *Hyla septentrionalis* (KU 89930) at levels of the cranial nerve foramina: (37) level of orbitonasal foramen; (38) level of optic foramen; (39) level of oculomotor foramen. Abbreviations: *c. scl.*, cartilaginous sclera; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *nas.*, nasal; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *orbnas. f.*, orbitonasal foramen; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *spheth.*, sphenethmoid; *sq.*, squamosal; *t. t. mar.*, taenia tecti marginalis; *tect. syn.*, tectum synoticum; *tym. r.*, tympanic ring.

mediately posterior to the anterior acoustic foramen and terminates anterior to the posterior margin of the juglar foramen.

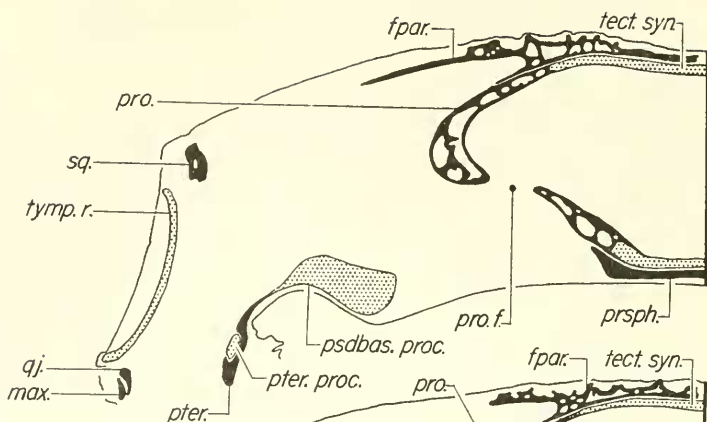
At the posterior level of the optic foramen, the prootic is ossified only laterally around the margins of the foramen. Dorsally, the tectum synoticum (Fig. 39) forms the posterior border of the frontoparietal fontanelle and the roof of the neurocranium. Ventrally, the floor of the neurocranium is cartilaginous. Posteriorly, ossification invades the cartilage of the prootic. At the anterior level of the prootic foramen, the tectum synoticum and the ventromedial part of the floor of the neurocranium are cartilaginous. Posteriorly, ossification invades the cartilage of the prootic. At the anterior level of the prootic foramen, the tectum synoticum and the ventromedial part of the floor of the neurocranium are cartilaginous. At the level of the anterior acoustic foramen posteriorly, the roof is cartilaginous. Ventrally, the cartilaginous floor of the neurocranium is restricted to a narrow medial strip which is flanked laterally by bone; laterally adjacent to the bone is cartilage which forms the lateral and ventrolateral parts of the otic capsule. Posteriorly, at the level of the jugular foramen, cartilage diminishes and is replaced by bone except laterally, dorsomedially and ventromedially. The pars externa plectri, pars interna plectri, pars ascendens plectri and operculum are cartilaginous. The distal tip of the crista parotica is cartilaginous. The pars media plectri is bony.

*The Articular Region.*—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenial bone. Posteriorly, the cartilage enlarges and moves into a position dorsomedial to the angulosplenial. The quadrate process first appears flanked by the ventral arm of the squamosal dorsally and the medial ramus of the pterygoid medially at the anterior level of the operculum. Slightly posterior, ossification invades the cartilage of the quadrate process. At approximately the mid-level of the operculum, the quadratojugal fuses with the ossification of the quadrate process. At the posterior level of the jugular foramen, the quadrate process loses its ossification; in subsequent sections the pterygoid and squamosal terminate.

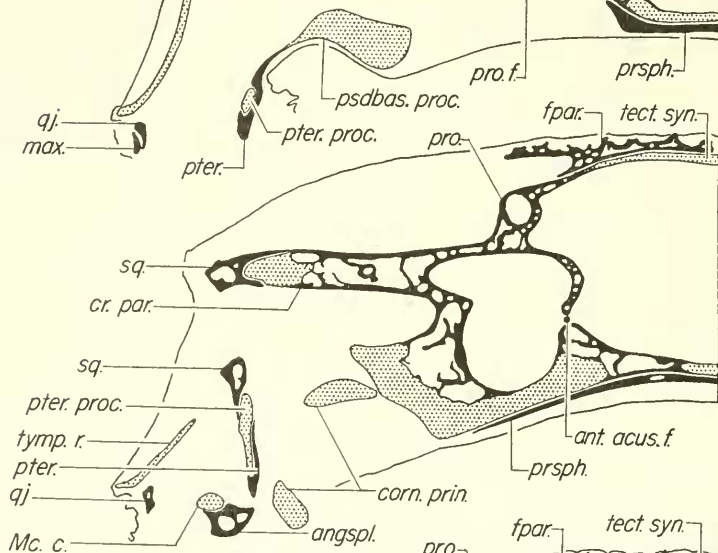
*Remarks.*—There is considerable variation in the development of dermal roofing bones in *Hyla septentrionalis* (Pl. 4a, b). Typically, adult females are more heavily ossified than males. The most striking differences between adult males and females are the fusion of the anterior arm of the squamosal with the maxillary, and the articulation of the posterolateral corners of the frontoparietal with the squamosal in the females. Moreover, some large females bear palatine and parasphenoid odontoids which are not usually characteristic of males. The prevomerine dentigerous processes are slightly curved in some large females.

*Hyla septentrionalis* is a member of a group of large West Indian tree frogs composed of *Hyla vasta*, *H. brunnea*, *H. lichenata*, and *H. dominicensis*. *Hyla vasta* is one of the largest and is the most divergent osteologically; the skull is not casqued or co-ossified. However, the general shape and structure of the skull is similar to a young *Hyla septentrionalis* before extensive dermal modifications develop. The maxillary is robust and bears a large pars facialis. The nasals are moderately large and articulate firmly with the posterior process of the pars facialis of the maxillary. The sphenethmoid is well ossified. The frontoparietals do not converge medially; thus, a frontoparietal fontanelle is exposed dorsally. The squamosal is moderately weak; the anterior arm does not articulate with the maxillary. The pterygoid is robust and articulates firmly with the

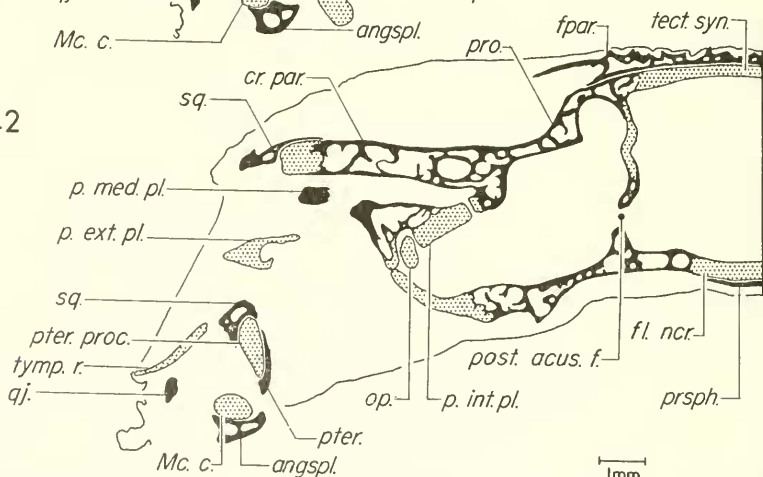
40



41



42



1mm

FIGS. 40-42. Transverse sections through the skull of *Hyla septentrionalis* (KU 89930) at levels of cranial nerve foramina: (40) level of prootic foramen; (41) level of anterior acoustic foramen; (42) level of posterior acoustic foramen. Abbreviations: *angspl.*, angulosphenial; *ant. acus. f.*, anterior acoustic foramen; *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *op.*, operculum; *p. ext. pl.*, pars externa plectri; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *psdbas. proc.*, pseudobasal process; *qj.*, quadrate-jugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

prootic. The parasphenoid does not bear odontoids. Anteriorly, the palatines are moderately developed; they bear an inconspicuous and smooth posteroventral ridge. The prevomers are well developed; the posterior dentigerous part of the prevomer is massive and only slightly curved. (see Table 1).

Externally, the skull of *Hyla dominicensis* is almost indistinguishable from that of *Hyla septentrionalis*. The skull is heavily casqued and partly or wholly co-ossified. The dermal sphenethmoid is proportionally somewhat larger than the dermal sphenethmoid of *H. septentrionalis*; thus, the length of the medial convergence of the nasals anterior to the sphenethmoid is noticeably shorter in *H. dominicensis*. Posteriorly, the frontoparietals extend over, and curve posteroventrally, around the occipital region. The posterior arm of the squamosal is short and very poorly developed. Ventrally, *H. dominicensis* lacks the firm articulation of the medial branch of the pterygoid with the prootic, which is characteristic of *H. septentrionalis* also. Like *H. vasta*, *H. dominicensis* bears a smooth parasphenoid and palatine with smooth posteroventral ridges. The dentigerous process of the prevomers are less massive than those of *H. vasta* and about equal in development to those of *H. septentrionalis*; the dentigerous processes are slightly curved (see Table 1).

*Hyla brunnea* is a large frog, approaching *H. lichenata* in size. The skull has a well developed casque, is partly co-ossified, and is easily distinguished from those of *H. vasta*, *H. septentrionalis*, and *H. dominicensis* by the shape of the snout. In dorsal view the snout of *H. brunnea* is acuminate and protuberant, whereas the snouts of the other species are rounded or truncate. Osteologically, the shape of the snout in *H. brunnea* is due to the projection of the nasals anteriorly between the external nares. The nasals bear more distinct canthal ridges than in *H. septentrionalis*, *H. dominicensis*, and *H. vasta*; the condition of the canthal ridges accentuates the pointed shape of the snout. In lateral view, the alary processes of the premaxillary of *H. brunnea* are inclined slightly anteriorly, whereas in the other three species, the alary processes are vertical or inclined slightly posteriorly. The dermal sphenethmoid is proportionally slightly smaller than the dermal sphenethmoids of *H. septentrionalis*, and *H. dominicensis*. The frontoparietal is well developed. The frontoparietal extends posterolaterally to the posterior arm of the squamosal; posteriorly it extends over and curves posteroventrally around the occipital region as the frontoparietal does in *H. dominicensis*. The anterior arm of the squamosal does not articulate with the maxillary. The posterior arm of the squamosal is better developed than that of *H. dominicensis*, but not as well developed as that of *H. septentrionalis*. The ventral arm of the squamosal is robust. The pterygoid is robust; its medial arm articulates with the prootic. The parasphenoid bears small, inconspicuous odontoids and the palatine a conspicuous and smooth ventral ridge. The prevomers are large and well ossified. The dentigerous processes of the prevomers are strongly curved. (see Table 1).

There are no skeletal preparations of *Hyla lichenata* available for examination. Dunn (1926:123) suggested that *H. lichenata* is more closely related to *H. brunnea* than to *H. dominicensis* and *H. septentrionalis* because “. . . the Jamaican species [*Hyla lichenata*, *marianae*, and *wilderi*] all agree with *brunnea* in the prominent and terminal nostrils, which is the only essential feature differentiating the primitive Jamaican form from the primitive Hispaniolan *dominicensis*. The Hispaniolan species [*Hyla vasta*, *heilprini*, and *pulchrilineata*] agree with *dominicensis* in this feature.” Dunn’s statement “prominent and

terminal nostrils" is more satisfactorily interpreted by the structure of the snout and anterior end of the skull in *H. brunnea*. If the external shape of the snout of *H. lichenata* closely resembles that of *H. brunnea*, it seems logical to assume that structurally these two species are similar and that both probably differ similarly from *H. dominicensis*, *septentrionalis*, and *vasta*. *Hyla lichenata* is a larger frog than *H. brunnea*. The skull is heavily casqued and completely co-ossified. Thus as Dunn (1926:124) suggested, *H. lichenata* may be "an overgrown *brunnea*."

### Cranial Morphology of *Osteocephalus taurinus*

The skull of *Osteocephalus taurinus* (Pl. 5a, b) is slightly broader than long, or as broad as long. The snout in dorsal view is moderately truncate. Most of the dorsal surfaces of the skull are rugose. The overlying skin is thin and characterized by a thin layer of dense connective tissue, the presence of which precludes the complete development of integumentary-cranial co-ossification. The development of rugosities on the surface of dermal bones and the presence of a poorly developed, dense, connective tissue layer overlying the bone suggest that the lower part of the connective tissue has been transformed into membranous bone. Thus, co-ossification is partial or incomplete in *Osteocephalus*, and the skin is freely movable on the surface of the head. *Osteocephalus* lacks a prenasal and internasal. There are no labial flanges or an occipital crest. A dermal sphenethmoid is present. The frontoparietals bear a small, upturned flange; the frontoparietal does not extend over the crista parotica posterolaterally. The prevomerine teeth are angled (see Table 1). The anterior arm of the squamosal extends less than one-half the distance to the maxillary. The vocal sacs are paired, lateral, and located behind the angles of the jaws.

*The Olfactory Region.*—The premaxillaries are narrowly separated medially by connective tissue. Laterally, the premaxillary is separated from the pars palatina and pars dentalis of the maxillary by an area of dense connective tissue. An extremely small and inconspicuous palatine process is present postero-medially on the premaxillary. The alary processes of the premaxillaries are widely separated medially. They are inclined posteriorly at approximately an 80-degree angle. The processes are straight and approximately two and one-half times as long as the depth of the pars dentalis of the premaxillary.

In ventral view (Pl. 5b), the prevomer lies lateral to the mid-line of the skull, and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer lies posterior to the premaxillary. The posterior, dentigerous part of the prevomer is angled (see Table 1). The prevomer bears well developed lateral wings that form the anterior, medial, and posteromedial margins of the internal naris. Internally, the prevomer bears a small dorsal extension that supports the olfactory eminence.

The palatine is a narrow, thin bone which lies posterior to the internal naris. The distal end is slightly expanded and is lodged in connective tissue dorsal to the pars palatina of the maxillary and adjacent to the anterior maxillary process. The delicate proximal end lies ventral to the lateral edge of the sphenethmoid and is separated from the sphenethmoid by a thin layer of connective tissue. The palatine bears a small posteroventral ridge which has an irregular surface.

The nasal is moderately large (Pl. 5a). Anteriorly, the nasal lies dorsally adjacent to the tips of the alary processes of the premaxillary. The nasal arches

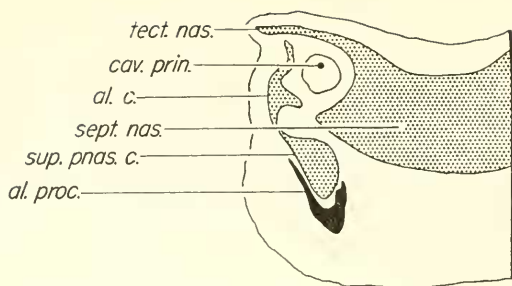
posterodorsally over the external naris and terminates posteroventrally in a slim maxillary process. The maxillary process articulates with the posterior process of the pars facialis of the maxillary. The nasals converge anteromedially to the dorsally exposed part of the sphenethmoid. Posterolaterally the nasal articulates with the frontoparietal and posteromedially with the dermal sphenethmoid. The dorsal surface of the nasal is slightly rugose. The canthal ridge is distinct; it extends along the lateral edge of the bone to the anterodorsal corner of the orbit. The margins of the nasal are smooth.

The maxillary is well developed but not robust. It does not bear a labial flange and the outer surface of the bone is smooth. The maxillary bears a well developed pars facialis anterior to the orbit; all margins of the pars facialis are free except for the posterior process; the latter articulates with the maxillary process of the nasal to form a bony anterior margin to the orbit. Medially, the pars palatina of the maxillary is small and extends the length of the bone dorsal to the pars dentalis. The maxillary articulates firmly with the quadratojugal posteriorly and terminates laterally adjacent to the quadratojugal at the level of the jugular foramen.

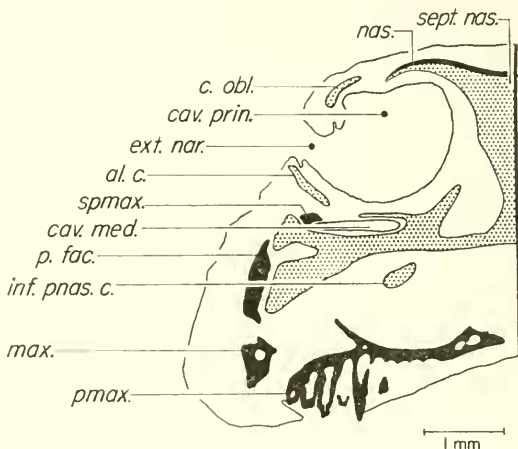
The anterior end of the septum nasi appears between the alary processes of the premaxillaries. Slightly posterior, the anterolateral corners of the tectum nasi appear dorsal to the alary processes; in subsequent sections, the tectum expands medially and fuses with the septum nasi posterior to the dorsal part of the alary process (Fig. 43). The anterior end of the superior prenasal cartilage lies adjacent to the posterodorsal surface of the alary process. In posterior sections, the superior prenasal cartilage extends dorsally and fuses with the anteroventral surface of the alary cartilage (Fig. 43). The anterior end of the alary cartilage lies just posterior and ventrolateral to the anterior corner of the tectum nasi. Posteriorly, the alary cartilage expands ventromedially and fuses with the solum nasi for a short distance to completely encase the anterior end of the cavum principale in cartilage. At the level of the foramen for the ramus externus and medius narius the alary cartilage loses its connection with the solum nasi, gradually diminishes in size and terminates at the posterior margin of the external naris. The anterior end of the inferior prenasal cartilage lies at the base of the posterior surface of the alary process of the premaxillary. From its anterior tip, the prenasal cartilage extends posterodorsally and fuses with the solum nasi at the level of the planum terminale. A crista subnasalis is present. The anterior end of the cavum principale (Fig. 43) lies between the alary cartilage and septum nasi, anterior to the level of the pars dentalis of the premaxillary. The cavum medium (Fig. 44) appears posteriorly at the level of the external naris and pars dentalis of the premaxillary just posterior to the foramen ramus externus and medius narius. The anterolateral recess of the cavum inferius appears ventrolateral to the cavum medium; the medial recess appears slightly posterior to the lateral recess, at the level of the palatine process of the premaxillary.

The nasal region is only moderately ossified. There is a gap between the anterior end of the prevomer and the premaxillary; the anterolateral and lateral margin of the nasal does not articulate with the pars facialis of the maxillary. The anterior level of perichondral ossification of the septum nasi lies at the anterior end of the prevomer, or near the posterior terminus of the planum terminale. Posterior to this level, ossification increases gradually in the dorsal part of the septum, and progresses in a posteroventral direction. At the level

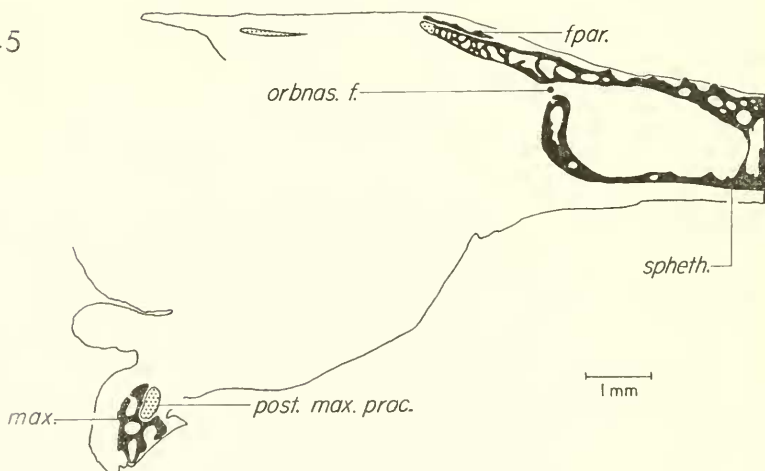
43



44



45



FIGS. 43-45. Transverse sections through the anterior end of the skull of *Osteocephalus taurinus* (KU 92243): (43) level of alary process of premaxillary; (44) anterior level of cavum medium and septomaxillary; (45) level of orbitonasal foramen. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *c. obl.*, cartilago obliquus; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *ext. nar.*, external nares; *inf. pnas. c.*, inferior prenasal cartilage; *max.*, maxillary; *nas.*, nasal; *orbnas. f.*, orbitonasal foramen; *p. fac.*, pars facialis of maxillary; *pmax.*, premaxillary; *post. max. proc.*, posterior maxillary process; *sept. nas.*, septum nasi; *spheth.*, sphenethmoid; *spmax.*, septomaxillary; *sup. pnas. c.*, superior prenasal cartilage; *nect. nas.*, tectum nasi.

of the anterior margin of the internal nares, the septum nasi is completely ossified. The solum is ossified a short distance posterior to the anterior margin of the internal nares.

The anterior ramus of the septomaxillary is broad and thin and lies dorso-lateral to the cavum medium. It expands medially first, and comes to lie between the lamina superior and lamina inferior. In subsequent sections, the septomaxillary extends posterolaterally around the lateral end and ventrolateral edge of the cavum medium. The ventral ramus thus formed loses its lateral connection with the dorsal, anterior ramus. In sections posterior to this bifurcation, the horizontally-oriented anterior ramus develops a high dorsal flange, the dorsal ramus of the septomaxillary. A short distance posterior to the appearance of the dorsal ramus, the dorsal part of the septomaxillary bifurcates into medial and lateral rami. The former is associated with the distal edge of the lamina superior, and the latter bears the dorsal ramus. In more posterior sections, the medial ramus diminishes in size whereas the lateral ramus turns approximately 90 degrees from a vertical to a more dorsal, horizontal orientation to accommodate the confluence of the cava medium and principale. Slightly posterior to the latter level, the medial ramus of the septomaxillary terminates and the distal part of the cavum medium diverges laterally as the nasolacrimal duct. The dorsal and ventral rami of the septomaxillary then fuse, diminish in size and terminate in a short distance.

*The Sphenethmoid and Orbital Region.*—The frontoparietals converge medially throughout their lengths posterior to the dermal sphenethmoid (Pl. 5a). Anteriorly, the frontoparietal articulates with the posterior margin of the dermal sphenethmoid medially and the posterior margin of the nasal laterally. The frontoparietal forms a narrow, upturned supraorbital shelf or flange laterally; the flange extends posteriorly over the prootic and terminates at the posterior margin of the frontoparietal dorsal to the exoccipital. The frontoparietal does not bear an occipital crest posteriorly, and it does not extend laterally over the crista parotica. The dorsal surface of the frontoparietal is slightly rugose but the overlying skin is not fused with the bone below. The distal margins of the frontoparietal are smooth.

The dermal sphenethmoid is pentagonal in shape; the anterior end is acuminate and the posterior end is flat. The bone lies posteromedial to the nasals and anteromedial to the frontoparietals. The dorsal surface of the dermal sphenethmoid is moderately rugose and bears a reticulate pattern of bony ridges, but the overlying skin is not fused with the bone below. The dorsally exposed sphenethmoid is confluent with the underlying endochondral sphenethmoid as previously described for *Tripurion petasatus* and *Hyla septentrionalis*.

The endochondral sphenethmoid is in synosteotic continuity with the septum nasi anteriorly. Posterior to the transition zone between the planum antorbitale and the sphenethmoid, the sphenethmoid is completely bony (Fig. 45). Cartilage appears at the distal tip of the anterolateral wing of the sphenethmoid a short distance anterior to the level of the orbitonasal foramen; this cartilage expands laterally in posterior sections and terminates posteriorly at the level of the articulation of the nasal and frontoparietal. The margins of the orbitonasal foramen are bony (Fig. 45). Posterior to the terminus of the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. Anteriorly, the margins of the

fontanelle are bony; posteriorly, near the level of the optic foramen, the margins of the foramen are cartilaginous (*taenia tecta marginalis*) (Fig. 46). At the same level, cartilage appears in the dorsolateral parts of the sphenethmoid, and a short distance posterior, in the floor of the sphenethmoid.

The anterior end of the parasphenoid (Pl. 5b) lies at a level between the orbitonasal foramen and the posterior terminus of the dermal sphenethmoid. The parasphenoid lies ventral to the sphenethmoid and prootic and forms a bony bridge of support for the neurocranial floor at the level of the synchondrotic union of the sphenethmoid and prootic. The parasphenoid is narrowly separated from dorsally adjacent bones and cartilages by dense connective tissue. Posteriorly and ventral to the prootic, the bone bears a delicate and inconspicuous odontoid structure.

The bursa angularis oris is well developed; it lies in the posterior part of the orbit parallel to the length of the jaw and between the maxillary and pterygoid bones. The lymphoid tissue of the gland is encased in a connective tissue capsule. The bursa is tubular and closed at the anterior end. A short distance posteriorly, a longitudinal aperture opens from the central lumen of the bursa into the oral cavity. At the latter level, the lumen of the gland loses its smooth surface and forms plicae and folds internally.

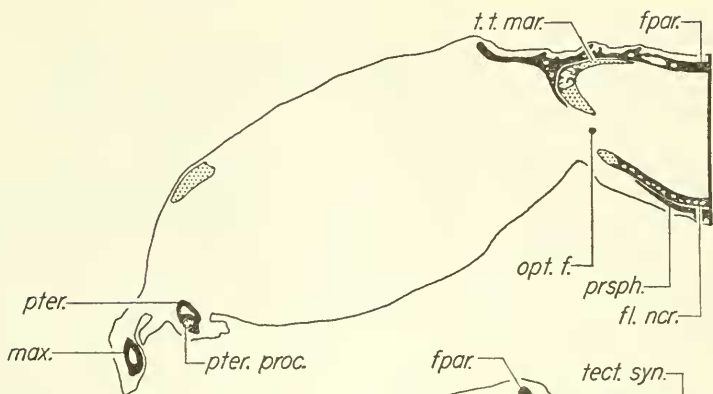
*The Otic and Occipital Regions.*—The squamosal is a moderately delicate bone. The anterior arm is slender and extends less than one-half the distance from the dorsal union of the three squamosal arms to the maxillary. The posterior arm of the squamosal is longer than the anterior arm. In dorsal view, the posterior arm articulates medially and broadly overlaps the crista parotica. The ventral arm is delicate; posteroventrally, it lies between the posterior ramus of the pterygoid medially and the quadratojugal laterally. The surfaces of the squamosal are smooth and not co-ossified.

The pterygoid (Pl. 5b) is robust. The anterior ramus is only moderately long; its anterior end lies adjacent to the posterior maxillary process at approximately the mid-level of the orbit. The medial ramus is long, well developed, and articulates firmly with the anteroventral corner of the otic capsule ventrally. The posterior ramus articulates with the ventral half of the ventral arm of the squamosal.

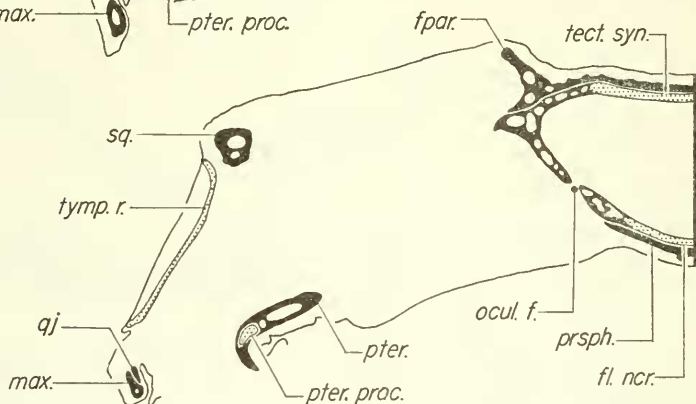
The quadratojugal is long and slender. The anterior end of the quadratojugal articulates medially with the maxillary at the mid-level between the optic and oculomotor foramina. Just posterior to the terminus of the maxillary, the ossification of the quadratojugal invades the cartilage of the quadrate process.

The anterior margin of the optic foramen (Fig. 46) is bony. Dorsally, the lamina perpendicularis of the frontoparietal forms a bony margin, whereas ventrally, the edge of the foramen is cartilaginous. Posteriorly, the prootic forms a bony margin to the optic foramen. The trochlear foramen lies dorsally adjacent to the lamina perpendicularis at the frontoparietal within the bony margins of the optic foramen. The trochlear and optic nerves are separated by connective tissue. The oculomotor foramen (Fig. 47) lies posterior and ventral to the optic foramen and a short distance anterior to the prootic foramen (Fig. 48). The margins of the oculomotor and prootic foramina are bony. There are two acoustic foramina (Figs. 49-50); both have bony margins. The jugular foramen (Fig. 51) is formed in bone posteriorly.

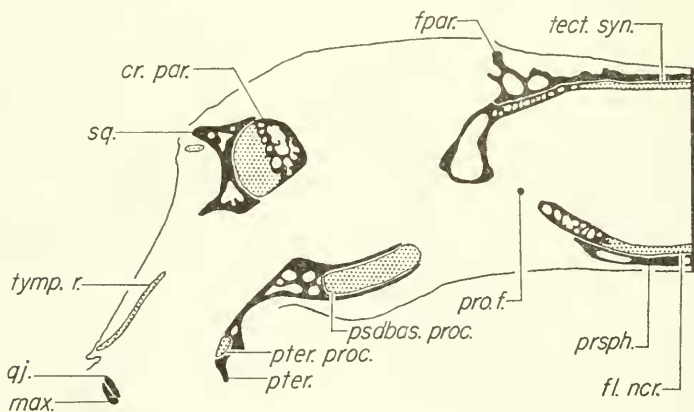
46



47



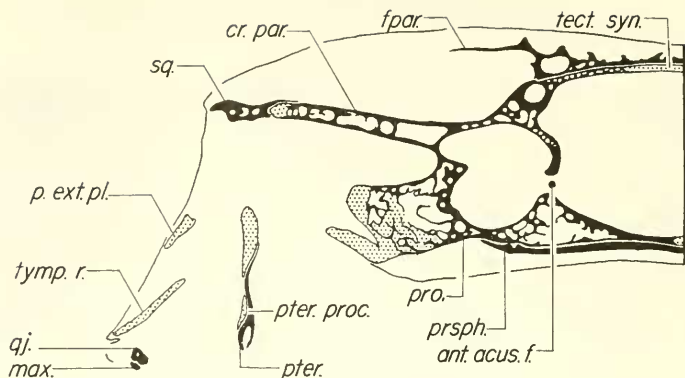
48



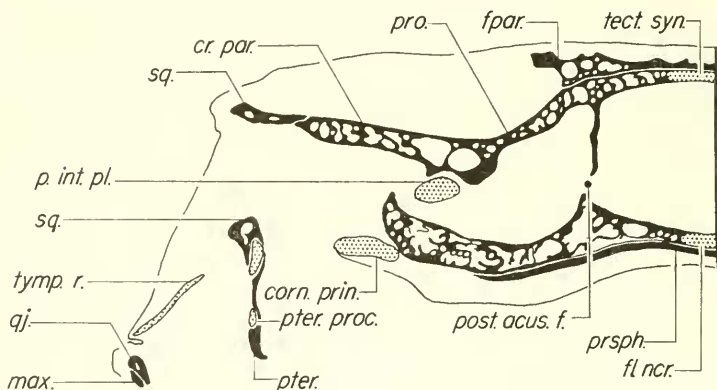
1 mm

FIGS. 46-48. Transverse sections through skull of *Osteocephalus taurinus* (KU 92243) at levels of cranial nerve foramina: (46) level of optic foramen; (47) level of oculomotor foramen; (48) level of prootic foramen. Abbreviations: cr. par., crista parotica; fl. ncr., floor of neurocranium; fpar., frontoparietal; max., maxillary; ocul. f., oculomotor foramen; opt. f., optic foramen; pro., prootic; pro. f., prootic foramen; prsph., parasphenoid; psdbas. proc., pseudo-basal process; pter., pterygoid; pter. proc., pterygoid process; qj., quadratojugal; sq., squamosal; t. t. mar., taenia tecti marginalis; tect. syn., tectum synoticum; tym. r., tympanic ring.

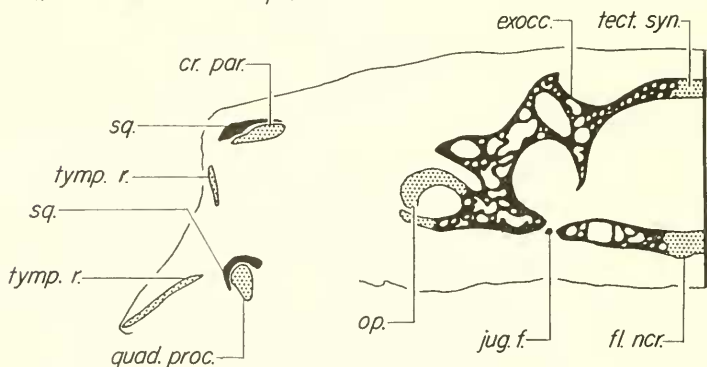
49



50



51



1 mm

FIGS. 49-51. Transverse sections through the skull of *Osteocephalus taurinus* (KU 92243) at levels of cranial nerve foramina: (49) level of anterior acoustic foramen; (50) level of posterior acoustic foramen; (51) level of jugular foramen. Abbreviations: ant. acus. f., anterior acoustic foramen; corn. prin., cornu principalis; cr. par., crista parotica; exocc., exoccipital; fl. ncr., floor of neurocranium; fpar., frontoparietal; jug. f., jugular foramen; max., maxillary; op., operculum; p. ext. pl., pars externa plectri; post. acus. f., posterior acoustic foramen; pro., prootic; prsph., parasphenoid; pter., pterygoid; pter. proc., pterygoid process; qj., quadrate process; quad. proc., quadrate process; sq., squamosal; tect. syn., tectum synoticum; tymp. r., tympanic ring.

The antermost part of the otic region is the dorsolateral corner of the otic process which lies medially adjacent to the posterior arm of the squamosal at a level just posterior to the oculomotor foramen (Fig. 48). At the posterior margin of the prootic foramen, the crista parotica is complete and the pterygoid and pseudobasal process are fused to the ventral part of the otic capsule; the otic process is fused to the ventral part of the otic capsule; the otic process is fused to the pseudobasal process ventrally for a short distance at this level. The pars ascendens plectri, pars externa plectri, pars interna plectri, and cornu principalis of the hyale lie at the level of the anterior acoustic foramen. The pars media plectri lies at the level of the posterior acoustic foramen. The operculum lies at the posterior level of the posterior acoustic foramen (Fig. 50) and terminates posterior to the jugular foramen.

At the posterior level of the optic foramen, the prootic is ossified laterally; the tectum synoticum and the floor of the neurocranium are cartilaginous. In posterior sections, ossification progresses ventrolaterally and invades the neurocranial floor. At the posterior margin of the prootic foramen, bone has replaced the lateral parts of the tectum synoticum; the otic capsule is completely ossified except for the ventrolateral corner, and only a narrow ventromedial strip of the neurocranial floor remains cartilaginous. Posteriorly, the tectum becomes increasingly ossified until only a narrow dorsomedial strip remains at the posterior margin of the posterior acoustic foramen. The ventrolateral edge of the otic capsule is cartilaginous posterior to the terminus of the operculum. The distal tip of the crista parotica, the pars ascendens plectri, pars externa plectri, pars interna plectri, and operculum are cartilaginous, whereas the pars media plectri is bony.

*The Articular Region.*—Anterior to the articular region, Meckel's cartilage lies lateral to the angulosplenic bone. Posteriorly, at the level of the operculum, the cartilage assumes a position dorsal to the angulosplenic bone, enlarges slightly in size and becomes partly ossified. At the posterior level of the jugular foramen, the quadrate process is cartilaginous, and bordered dorsally by the ventral arm of the squamosal and medially by the posterior ramus of the pterygoid; at this level, the quadratojugal lies ventrolateral to the quadrate process. A short distance posterior, bone invades the cartilage of the quadrate process. The quadratojugal does not fuse with the ossified quadrate process until the mid-level of the occipital condyles. At the posterior levels of the occipital condyles, the ventral arm of the squamosal and the posterior ramus of the pterygoid terminate. Posteriorly, the quadrate process loses its ossification.

*Remarks.*—The morphology of *Osteocephalus* is similar to that of the widespread (México to Argentina) lowland species, *Phrynohyas venulosa* (compare Fig. 52a, b and Pl. 5a, b). Both species have paried, lateral vocal sacs behind the angles of the jaws. Cranially, the differences between the two species are minor. The septomaxillary of *Phrynohyas* is like that described for *Tripion* and *Smilisca* and differs from that of *Osteocephalus*; the ventral ramus of the septomaxillary is not attached to the anterolateral corner of the septomaxillary. The dermal roofing bones are expanded; the nasals are nearly indential to those of *Osteocephalus*, but the frontoparietals lack a supraorbital flange. The dorsum of the skull of *Phrynohyas* is not co-ossified; consequently, a dermal sphenethmoid is absent. Both species lack a complete squamosal arch. The posterior arm of the squamosal of *Osteocephalus* bears a broader articulation with the crista parotica than in *Phrynohyas*.

Ventrally (compare Fig. 52b and Pl. 5b), the most noticeable difference between the two species is the shape of the dentigerous processes of the prevomers. The processes are large in both species; they are slightly curved in *Phrynohyas* and angular in *Osteocephalus*. The palatine of *Osteocephalus* bears minute denticulations laterally, whereas the palatine of *Phrynohyas* is smooth; the palatines are otherwise the same. *Osteocephalus* bears an exceptionally small rugosity, consisting of two or three odontoid-like structures, near the base of the parasphenoid; the parasphenoid of *Phrynohyas* is edentate. In both species, the basal wings of the parasphenoid are posteriorly inclined. The pterygoids of *Osteocephalus* and *Phrynohyas* bear medial rami which articulate firmly with the prootics; the anterior rami of the pterygoids terminate adjacent to the maxillary in the mid-orbital region. The bursa angularis oris of *Phrynohyas* is like that of *Osteocephalus*.

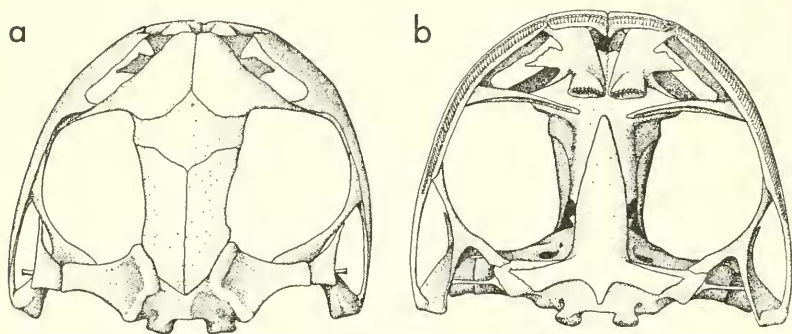


FIG. 52. Skull of *Phrynohyas venulosa* (KU 68177)  $\times 2.6$ : (a) dorsal view; (b) ventral view.

### Cranial Morphology of *Trachycephalus nigromaculatus*

The skull of *Trachycephalus* is as long as wide (Pl. 6a). The snout in dorsal view is truncate and bears a medial "notch." All dorsal surfaces of the dermal bones are sculptured into rugosities and prominent, irregular ridges. The distal margins of dermal bones are rugose or spinose; distal spines are best developed in the orbital and occipital regions. The skull of *Trachycephalus* is characterized by the absence of a prenasal, the presence of a dermal sphenethmoid, and the lack of labial flanges on the maxillary and premaxillary. The pars facialis of the maxillary articulates only with the ventrolateral corner of the nasal. The dorsal surface of the dermal bones are extremely rugose. The prevomerine teeth are straight. The palatine and parasphenoid bear odontoid structures. The vocal sacs are paired, lateral, and located behind the angles of the jaws.

*The Olfactory Region.*—The premaxillaries are robust and lie anteromedial to the maxillaries. The alary processes of the premaxillaries are greatly expanded and co-ossified anteriorly. Anterodorsally, the alary process articulates with the anterior tip of the nasal. Dorsomedially, the process forms the anterior margin of the external nares. Laterally, the alary process articulates with the pars facialis of the maxillary, and medially the processes articulate with one

another. The alary processes are concave posteriorly and are oriented approximately vertically. The pars palatina of the premaxillary is well developed and the posteromedial palatine process is conspicuous.

In ventral view (Pl. 6b), the prevomer lies lateral to the midline of the skull and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer lies dorsolateral to the premaxillary. The prevomer bears well developed lateral wings which form the anterior and medial margins of the internal naris. The prevomers converge medially just anterior to the prevomerine teeth; the dentigenous processes are slightly curved in a transverse plane. Internally, the prevomer provides bony support for the olfactory eminence. The prevomer is separated from the sphenethmoid and the solum nasi by a thin layer of dense connective tissue.

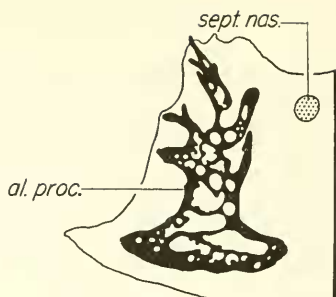
The palatine is a robust bone which lies posterior to the internal naris. The broad, distal end is lodged in connective tissue dorsal to the pars palatina of the maxillary and adjacent to the anterior maxillary process. The proximal end is pointed and lies ventral to the sphenethmoid and posterior to the prevomer. The palatine is separated from the sphenethmoid by a thin layer of dense connective tissue. The palatine bears a series of odontoids along a prominent ventral ridge.

The nasals are large. The anterior end of the nasal is blunt and articulates with the dorsal margin of the alary process of the premaxillary. Laterally the nasal arches over the external nares and articulates posteriorly and ventrolaterally with the pars facialis of the maxillary at the corner of the orbit. The nasal forms the anterior margin of the orbit. It articulates with the frontoparietal dorsolaterally and the dorsally exposed dermal sphenethmoid dorsomedially. The nasals converge medially anterior to the dermal sphenethmoid. The canthal ridge is distinct. The ridge extends from the anterior end of the nasal along the lateral margin to the anterodorsal corner of the orbit. The entire surface of the nasal is involved in the integumentary-cranial co-ossification. Dorsally, near the orbit, the surface of the nasal is rugose. The rest of the nasal is marked by prominent bony ridges. The ridges are rough and form a radial pattern from the rugose area.

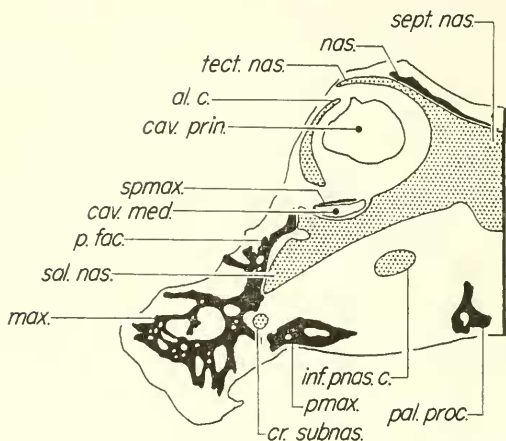
The maxillary is moderately robust, but lacks a labial flange. The pars facialis of the maxillary is well developed. It is largest anterior to the orbit. Anteriorly, the pars facialis articulates with the alary process of the premaxillary and forms the ventral margin of the external naris. Posterior to the external naris, the dorsal edge of the pars facialis is free; it articulates with the maxillary process of the nasal at the anterior margin of the orbit. The pars facialis diminishes in size ventral to the orbit, but it is conspicuous along the entire length of the maxillary. The pars palatina of the maxillary is well developed and extends from the anterior end of the bone posteriorly to the level of termination of the pars dentalis. Posteriorly, the maxillary firmly articulates with the quadratojugal which lies medial adjacent to the maxillary. The outer surface of the maxillary is co-ossified and highly rugose. There is an indistinct pattern of irregular bony ridges which radiate dorsally and anteriorly from the lower margin of the maxillary anterior to the orbit. Posterior and ventral to the orbit the outer surface of the maxillary is smooth, but the dorsal margin bears a series of small spines.

The anterior end of the septum nasi (Fig. 53) lies anterior to the nasals between the dorsomedial corners of the alary processes of the premaxillaries.

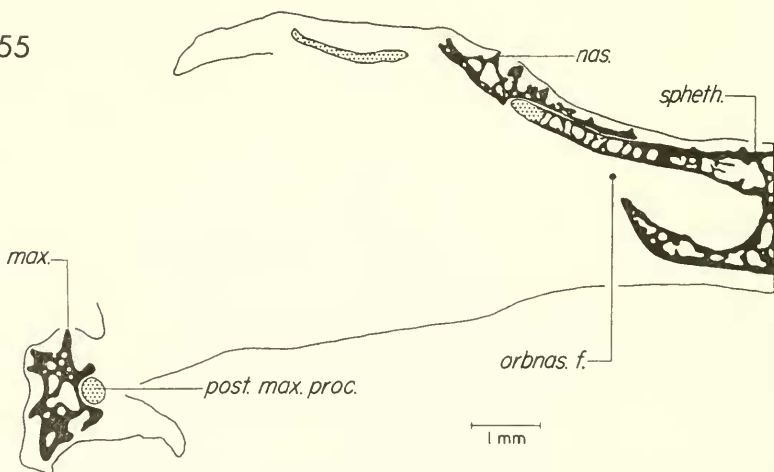
53



54



55



FIGS. 53-55. Transverse sections through the anterior end of the skull of *Trachycephalus nigromaculatus* (KU 100353): (53) level of the alary process of the premaxillary; (54) anterior level of cavum medium and septomaxillary; (55) level of orbitonasal foramen. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *ant. max. proc.*, anterior maxillary process; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *cr. subnas.*, crista subnasalis; *inf. pnas. c.*, inferior prenasal cartilage; *max.*, maxillary; *nas.*, nasal; *orb. nas. f.*, orbitonasal foramen; *p. fac.*, pars facialis of maxillary; *pal. proc.*, palatine process of premaxillary; *pmax.*, premaxillary; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spheth.*, sphenethmoid; *spmax.*, septomaxillary; *tect. nas.*, tectum nasi.

In subsequent sections, the inferior prenasal cartilage appears ventromedially at the base of the alary process. The anterior end of the superior prenasal cartilage lies adjacent to the posterodorsal surface of the alary process and is closely associated with the alary cartilage which emerges as an arcuate shaped cartilage from the dorsolateral corner of the massive superior prenasal cartilage. The tectum nasi appears posterior and dorsal to the anterior end of the alary cartilage. The tectum fuses medially with the septum nasi posterior to the alary process. The anterior end of the cavum principale lies ventral to the anterior end of the nasal at the posterior level of the pars dentalis of the premaxillary. The cavum is completely surrounded by the cartilage of the alary cartilage, the tectum, septum, and solum nasi. A short distance posterior, at the anterior level of the palatine process of the premaxillary (Fig. 54), the anterior end of the cavum medium appears ventral to the cavum principale. The anterior end of the cavum medium lies dorsal to the solum nasi instead of appearing within the cartilage as it usually does. In sections posterior to the anterior end of the cavum, the lamina superior appears as a small rod of cartilage dorsomedial to the cavum medium. Anteriorly, the lamina superior is disjunct from the crista intermedia at the posterior level of the palatine process of the premaxillary. The anterolateral recess of the cavum inferius appears in sections slightly posterior to the anterior end of the cavum medium; there is no anteromedial recess.

There is an unusual amount of ossification in the nasal region in the form of perichondral ossification of the nasal cartilages. The anterior end of the septum nasi, the inferior prenasal cartilage and the tectum nasi are perichondrally ossified. Farther posterior, the lateral margin of the alary cartilage is ossified and the entire dorsum and venter of the internasal septum posterior to the alary process of the premaxillary. The dorsal perichondral ossification of the septum nasi is replaced posteriorly by the nasal. At the anterior level of the septomaxillary and lamina superior, ossification appears in the membranous connective tissue overlying the cavum medium. The latter ossification is associated posteriorly with the venter of the lamina superior, and persists until the posterior level of the septomaxillary. Perichondral ossification of the venter of the solum disappears at the anterior end of the prevomer. At the level of the planum terminale, the septum nasi is perichondrally ossified dorsally, dorsolaterally, and ventrolaterally. Endochondral ossification lies in the dorsal part of the septum at the posterior level of the planum terminale. Posterior to this level, ossification spreads from the dorsal part of the septum ventrally. At the mid-level of the olfactory eminence, anterior to the internal naris, the entire septum is ossified, whereas the solum is cartilaginous. Shortly posterior to the anterior margin of the internal naris, ossification appears in the solum; the solum nasi is completely ossified at approximately the mid-level of the internal naris. The septum nasi is synosteotically united with the sphenethmoid posteriorly.

The anterior end of the septomaxillary (Fig. 54) is a thin bone horizontally oriented dorsal to the cavum medium. The septomaxillary expands laterally above, and then around, the cavum medium in posterior sections. The part of the septomaxillary lateral to the cavum terminates leaving the ventral ramus disjunct from the anterior ramus. Just posterior to this point, the anterior ramus of the septomaxillary diverges into a lateral and medial rami. The former develops a dorsal ramus. Somewhat posterior, at the level of the fusion of the

superior prenasal cartilage and solum nasi, the dorsal and ventral rami of the septomaxillary fuse and separate the newly formed nasolacrimal duct from the posterior part of the cavum medium. As the nasolacrimal duct diverges farther from the cavum in posterior sections, the ventral ramus diminishes in size and the septum becomes thicker and shorter vertically. The medial and lateral rami terminate, leaving only the dorsal ramus and the small ventral remainder of the septum. The latter gradually diminish in size and disappear.

*The Sphenethmoid and Orbital Region.*—The frontoparietals converge medially throughout their lengths. Anteriorly, the frontoparietal articulates with the nasal laterally and the dermal sphenethmoid medially. Anterolaterally, the frontoparietal forms a supraorbital shelf. Posterolaterally, the frontoparietal articulates with the anterior and posterior arms of the squamosal. Posteriorly, the frontoparietal terminates in spinose processes, but there is no occipital crest. Ventrally, the frontoparietal is attached to the exoccipital; it bridges the crista parotica from the exoccipital to the squamosal. The entire dorsal surface of the frontoparietal is involved in integumentary–cranial co-ossification. Medially, the bone is rugose. From the central rugosity, irregular bony ridges radiate out toward the distal margins of the bone. The outer edges of the bone bear series of small spines.

The dermal sphenethmoid (Pl. 6a) is a triangular shaped bone, centrally located at the anterior level of the orbit; the bone lies posteromedial to the nasals and anteromedial to the frontoparietals. The dermal sphenethmoid is completely involved in integumentary–cranial co-ossification. The dorsal surface of the bone is rugose. The dorsally exposed dermal sphenethmoid is confluent with the underlying endochondral sphenethmoid as previously described for *Tripriorion petasatus*, *Hyla septentrionalis*, and *Osteocephalus taurinus*.

The endochondral sphenethmoid is in synosteotic continuity with the septum nasi anteriorly. The margins of the orbitonasal foramen are bony (Fig. 55). At the level of the foramen, the sphenethmoid is completely bony except for the distal tip of the anterolateral wing. Posteriorly, this tip expands distally to form a broad supraorbital shelf ventral to the nasal (Fig. 55). The cartilage diminishes in size and disappears posterior to the level of the frontoparietal–nasal articulation. In sections posterior to the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. Posterolaterally, the margins of the fontanelle are formed by the cartilaginous taenia tecta marginalis. The cartilaginous tectum synoticum forms the posterior border of the fontanelle; the latter lies slightly anterior to the level of the optic foramen. Posterior to the level of the supraorbital, cartilaginous flange, cartilage appears again in the sphenethmoid at the level of the bursa angularis oris in the posterior part of the orbit. The cartilage lies in the dorsolateral corners of the braincase; in subsequent posterior sections, the cartilage spreads ventrally. At the level of the optic foramen, the sphenethmoid is composed entirely of cartilage except for a thin layer of internal perichondral ossification which lines the neurocranium.

The parasphenoid (Pl. 6b) is a robust bone which lies ventral to the sphenethmoid and prootic and forms a bony bridge between the two bones at the level of the optic foramen. The parasphenoid is separated from overlying bones by a thin layer of connective tissue. The acuminate anterior end of the parasphenoid lies posterior to the level of the orbitonasal foramen. Posteriorly, the

the parasphenoid widens and finally terminates in a broad, robust base ventral to the prootic. The parasphenoid bears a well developed longitudinal ventral ridge extending from a level slightly posterior to the anterior tip of the parasphenoid to a level slightly anterior to the optic foramen. Although the ridge is prominent, it is completely smooth and even, and thus bears little resemblance to similarly placed odontoid structures of other genera.

The bursa angularis oris is well developed and lies in the posterior part of the orbit. The bursa is tube-shaped and lies parallel to the jaw between the maxillary and pterygoid bones. Anteriorly, the bursa is a solid mass of lymphoid tissue. There is no central lumen within the bursa anterior to the level of the longitudinal aperture of the bursa into the oral cavity. The structure of the bursa angularis oris resembles that of *Triprion petasatus*.

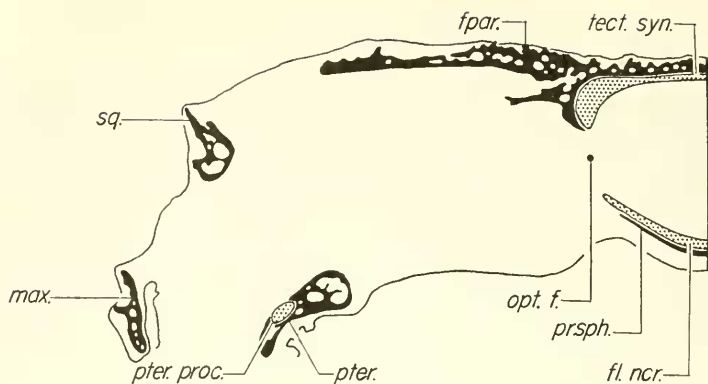
*The Otic and Orbital Regions.*—In dorsal view (Pl. 6a), the squamosal is a long bone which extends from the posterior edge of the orbit, along the postero-lateral margin of the frontoparietal to a level posterior to the posterior edge of the frontoparietal. The dorsal and lateral surfaces of the squamosal are ossified and highly rugose and spiny. The anterior arm of the squamosal is robust; it forms a part of the posterior margin of the orbit. Ventrally, the anterior arm terminates dorsal to the maxillary; it is connected to the maxillary by connective tissue but does not articulate with the maxillary. The posterior arm of the squamosal is as robust as the anterior arm and longer. The posterior arm articulates with the frontoparietal and crista parotica and extends posterior to these structures to the level of the posteroventral end of the ventral arm of the squamosal. The ventral arm of the squamosal is moderately robust. Ventrally, it terminates between the quadratojugal laterally and the pterygoid medially, and dorsal to the quadrate process.

The pterygoid is moderately robust. The anterior ramus lies adjacent to the posterior maxillary process at a level just posterior to the orbitonasal foramen. Posteriorly the pterygoid and pterygoid process diverge from the maxillary. The medial ramus is short, poorly developed and does not articulate with the prootic medially. The posterior ramus is robust; it articulates with the quadrate process and ventral arm of the squamosal posteriorly.

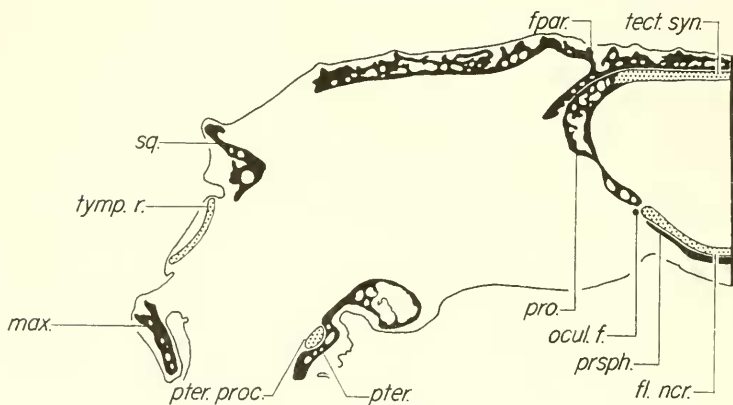
The quadratojugal is well developed. The anterior end lies medially adjacent to the maxillary at the level of the optic foramen. The quadratojugal increases in size posteriorly, whereas the maxillary diminishes in size. Posteriorly, the ossification of the quadratojugal invades the cartilage of the quadrate process.

The margins of the optic foramen (Fig. 56) are bony and formed by the lamina perpendicularis of the frontoparietal and perichondral ossification of the sphenethmoid and prootic. The trochlear foramen lies dorsally adjacent to the lamina perpendicularis of the frontoparietal, within the bony margins of the optic foramen. The trochlear and optic foramina are separated by connective tissue. The oculomotor foramen (Fig. 57) lies posteroventral to the optic foramen. Anterodorsally, the margins are bony and formed by the prootic. Ventrally, the margins are formed of bone (the parasphenoid and perichondral ossification of the floor of the neurocranium) and cartilage. The prootic foramen (Fig. 58) lies a short distance posterior and slightly dorsal to the oculomotor foramen; the two foramina are separated by connective tissue. The dorsal, ventral, and posterior margins of the prootic foramen are bony. The anterior acoustic foramen (Fig. 59) lies a short distance posterior to the prootic fora-

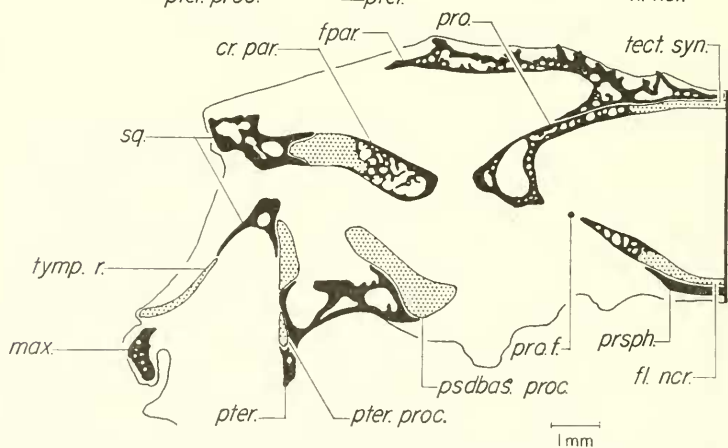
56



57



58



FIGS. 56-58. Transverse sections through the skull of *Trachycephalus nigromaculatus* (KU 100353) at levels of cranial nerve foramina: (56) level of optic foramen; (57) level of oculomotor foramen; (58) level of prootic foramen. Abbreviations: *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tym. r.*, tympanic ring.

men. The margins of the foramen are bony although only a thin bridge of bone separates the anterior acoustic foramen from the more posterior-lying posterior acoustic foramen (Fig. 60). The margins of the posteroventral jugular foramen (Fig. 61) are bony.

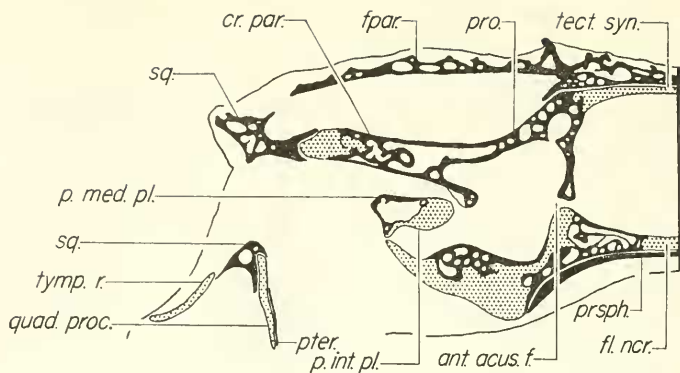
The pseudobasal process (Fig. 57) appears at the level of the optic foramen. The process lies ventrolateral to the neurocranium and increases in size posteriorly. The anterior end of the otic process lies encased in the anterior arm of the squamosal at the level of the oculomotor foramen. Posteriorly, both the otic and pseudobasal process expand medially. The otic process also extends posteroventrally to fuse with the pseudobasal process at the anterior level of the prootic foramen. At the mid-level of the prootic foramen the lateral block of cartilage formed by the otic and pseudobasal process is differentiated into the crista parotica dorsally (Fig. 58), the lateral edge of the otic capsule medially, and a lateral piece of cartilage which is continuous with the pterygoid process a short distance posteriorly. At the posterior level of the prootic foramen, the crista parotica extends from the dorsal head of the squamosal to the otic capsule medially and the cornu principalis of the hyale diverges postero-laterally from the ventrolateral edge of the otic capsule or pseudobasal process. Posterior to the level of the prootic foramen, the ventral edge of the otic capsule is complete.

The pars interna plectri, pars externa plectri, and the pars media plectri appear between the levels of the prootic and anterior acoustic foramen. The appearance of the pars externa plectri is followed by the appearances of the medial part of the pars media plectri and the pars interna plectri respectively. Posterior to the anterior level of the pars interna plectri, the distal parts of the pars media plectri appear. The anterior end of the operculum closes the foramen ovale. The posterior terminus of the operculum lies a short distance posterior to the posterior acoustic foramen. It is quite likely that a pars ascendens plectri is present also, but its position and nature cannot be determined from the specimen.

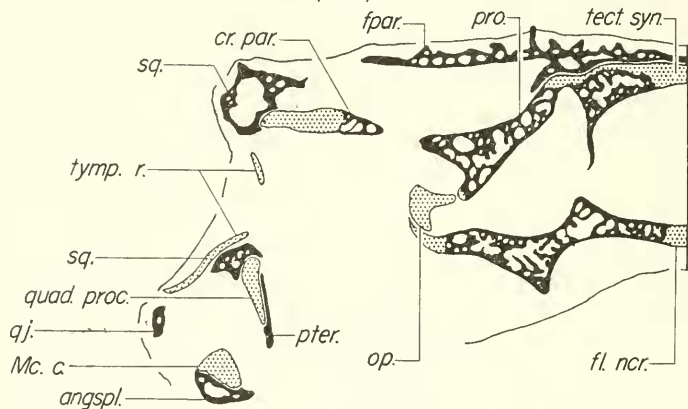
At the posterior level of the optic foramen, the prootic is ossified dorso-laterally; the tectum synoticum and the floor of the neurocranium are cartilaginous. Posteriorly, ossification invades the tectum synoticum and the floor of the neurocranium. At the level of the anterior acoustic foramen, the tectum synoticum and the ventromedial part of the floor of the neurocranium is cartilaginous. The ventral part of the otic capsule is cartilaginous with perichondral ossification. Bone invades cartilage posteriorly. At the level of the jugular foramen, the cranium is bony except for small dorso- and ventromedial pieces and the dorsum of the otic capsule. The distal end of the crista parotica is cartilaginous. The pars externa plectri, pars interna plectri, and operculum are cartilaginous, whereas the pars media plectri is bony.

*The Articular Region.*—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenial bone. Posteriorly, the cartilage assumes a position dorsal to the angulosplenial bone and then enlarges and comes to lie in close association with the posterior ramus of the pterygoid, the ventral arm of the squamosal and the quadrate process. The quadratojugal ossification invades the cartilage of the quadrate process at a level just anterior to the jugular foramen; the intrusive ossification and quadratojugal terminate a short distance posterior to the jugular foramen. At this level the ventral arm of the squamosal

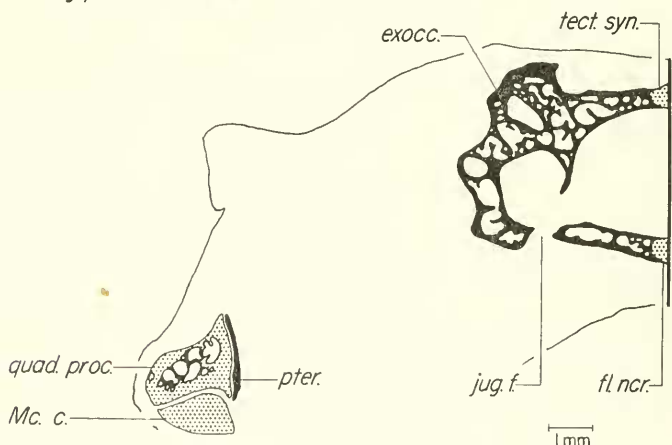
59



60



61



FIGS. 59-61. Transverse sections through the skull of *Trachycephalus nigromaculatus* (KU 100353) at levels of cranial nerve foramina: (59) level of anterior acoustic foramen; (60) level of posterior acoustic foramen; (61) level of jugular foramen. Abbreviations: *angsp.*, angulosplenial; *ant. acus. f.*, anterior acoustic foramen; *cr. par.*, crista parotica; *exocc.*, exoccipital; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *jug. f.*, jugular foramen; *Mc. c.*, Meckel's cartilage; *op.*, operculum; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadrate jugal; *quad. proc.*, quadrate process; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

and the posterior ramus of the pterygoid flank the quadrate process dorsolaterally and dorsomedially, respectively. Meckel's cartilage, which lies ventral to the quadrate process, is underlain by the angulosplenial bone.

### Cranial Morphology of *Trachycephalus jordani*

The skull of *Trachycephalus jordani* is only slightly longer than wide (Pl. 7a). The snout, in dorsal view, is truncate and bears a small medial "notch." All dorsal surfaces of the skull are involved in integumentary-cranial co-ossification. Dorsally, all dermal bones are sculptured in irregular rugosities and patterns of fine radial ridges. The distal margins of all dermal bones bear series of fine, denticulate spines. The posterior edge of the frontoparietal bears a moderately developed occipital crest. The skull of *Trachycephalus jordani* is characterized by its width and broadly rounded snout. A dermal sphenethmoid is present. The prenasal and internasal are absent, but the premaxillaries are heavily co-ossified and protrude anteriorly. The labial flanges are narrow. The prevomerine teeth are curved (see Table 1), and the palatine and parasphenoid bear well developed odontoid structures. The vocal sacs are paired, lateral and located behind the angles of the jaw.

This description is based on examination of the two available skeletal preparations. The attempt to make serial sections of one of the dried skulls was only moderately successful; thus, the following account is incomplete and is principally limited to the bony parts of the skull. Description of the septomaxillary, and the cartilaginous and other soft anatomical features of the cranium of *Trachycephalus jordani* is based on the examination of serial sections of a juvenile specimen.

*The Olfactory Region.*—The premaxillaries lie anterior to the nasals and anteromedial to the maxillaries. The alary process of the premaxillary is greatly enlarged and totally co-ossified. Ventrolaterally, the alary process articulates with the pars facialis of the maxillary; dorsally, it meets the anterior tip of the nasal. Between the two latter articulations, the alary process forms the bony anterior margin of the external naris. Medially, the alary process is narrowly separated by connective tissue from the adjacent process. The anterior surface of the process is spinose. The development of spines is heaviest near the base of the alary process. The latter results in the protrusion of a narrow labial flange anterodorsal to the pars dentalis of the premaxillary; this flange is continuous with a similar structure on the maxillary. The premaxillary bears an inconspicuous pars palatina and a moderately well developed palatine process.

In ventral view (Pl. 7b), the prevomer is large, lies lateral to the mid-line of the skull, and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer lies dorsal to the pars dentalis of the premaxillary and maxillary. The posterior dentigerous part of the prevomer is curved posterolaterally from the midline of the bone toward the palatine (see Table 1). The prevomer bears well developed lateral wings that form the anterior, medial, and posteromedial margins of the internal nares. Internally, the prevomer provides a bony support for the olfactory eminence.

The palatine is a moderately well developed bone which lies posterior to the internal nares. The broad, distal end is lodged in connective tissue dorsal to the pars palatina of the maxillary. The delicate, pointed proximal end lies ventral to the lateral edge of the sphenethmoid. The palatine bears a delicate postero-

ventral ridge with a serrate edge of fine denticulations; the ridge extends from the lateral edge of the sphenethmoid to the distal end of the palatine.

The nasal is extremely large. Anteriorly, the nasal terminates at the dorsal tip of the alary process of the premaxillary; the nasal forms the dorsal and posterior bony margins of the external naris. Laterally, the nasal lies closely adjacent to, but does not articulate with, the pars facialis of the maxillary; posterolaterally, it forms the bony anterior margin and anterior part of the supraorbital flange of the orbit. The nasals converge anteromedially to the dermal sphenethmoid. The posterior margin of the nasal articulates with the dermal sphenethmoid medially and the frontoparietal laterally. The dorsal surface of the nasal is completely involved in integumentary-cranial co-ossification. The nasal bears a well developed canthal ridge extending from the dorsal margin of the external naris to the anterodorsal corner of the orbit. The posterior part of the canthal ridge is rugose and pitted; bony ridges radiate from this area over the entire surface of the nasal.

The maxillary is moderately well developed. It bears a narrow labial flange throughout its length. All dorsal and lateral surfaces of the bone are co-ossified. The outer edge of the maxillary bears a series of small, spinose protuberances like those of the alary process of the premaxillary. The pars facialis bears prominent ridges. The pars facialis is well developed over the length of the maxillary. It is largest anterior to the orbit; ventral to the orbit, the pars facialis diminishes in size but it is still conspicuous. Medially, the maxillary bears a moderately developed pars palatina extending the length of the bone dorsal to the pars dentalis; the pars dentalis is best developed anterior to the orbit. Posteriorly, the quadratojugal lies medial to the maxillary. The posterior terminus of the maxillary lies just anterior to the articulation of the quadratojugal and ventral arm of the squamosal.

The anterior end of the septum nasi lies anterior to the nasals between the alary processes of the premaxillaries. In subsequent sections, the septum expands laterally posterior to the alary processes and the alary cartilage differentiates laterally from the septum. The superior prenasal cartilage lies adjacent to the posterodorsal surface of the alary process and ventromedial to the alary cartilage with which it is fused for a short distance. The tectum nasi appears at the same level at which the alary cartilage differentiates from the solum and is fused with the solum throughout its length. The anterior end of the cavum principale appears at a level near the base of the alary process and anterior to the pars dentalis of the premaxillary. The cavum is completely surrounded by the alary cartilage, the tectum nasi, solum nasi, and septum nasi. The anterior end of the cavum medium lies at the level of the external nares and the bases of the alary processes of the premaxillaries. The cavum medium appears within the cartilage of the solum nasi instead of dorsal to it, as the cavum does in *T. nigromaculatus*. The anterolateral recess of the cavum inferius lies ventrolateral to the cavum medium at the level of the posterior border of the external naris and anterior to the pars dentalis of the premaxillary. The inferior prenasal cartilage is well developed but short. It extends from the base of the alary process of the premaxillary posterodorsally to fuse with the solum nasi at the level of the pars dentalis of the premaxillary.

The anterior end of the septomaxillary lies dorsolateral to the cavum medium. In subsequent sections, the bone expands around the lateral edge of the cavum.

The anterior ramus bifurcates into lateral and medial branches at the level of the posterior margin of the external naris. The lateral branch bears a well developed dorsal ramus which appears just posterior to the divergence of the medial and lateral rami and just anterior to the separation of the lateral and ventral rami. Slightly anterior to the fusion of the inferior prenasal cartilage with the solum nasi, the dorsal and ventral rami of the septomaxillary unite to separate the nasolacrimal duct from the cavum medium. As the nasolacrimal duct diverges farther from the cavum in posterior sections, the ventral ramus diminishes in size and the septum becomes thicker and depressed. The medial and lateral rami terminate, leaving only the dorsal ramus and the small ventral remainder of the septum which gradually diminish in size and disappear.

*The Sphenethmoid and Orbital Region.*—The frontoparietal articulates anteriorly with the posterior margins of the dermal sphenethmoid and nasal. Laterally, the frontoparietal forms the posterior part of the supraorbital shelf and posterolaterally, it lies adjacent to the squamosal. The frontoparietals converge medially posterior to the dermal sphenethmoid. The posterior margin of the frontoparietal terminates in a small, spinose occipital crest. Ventral to the occipital crest, the frontoparietal lies dorsally adjacent to the exoccipital; laterally, it bridges the prootic from the exoccipital to the squamosal. The posterolateral corner of the frontoparietal bears a weak articulation with the posterior arm of the squamosal. The dorsal surface of the frontoparietal is involved in integumentary-cranial co-ossification. Medially, the bone is rugose and pitted. Peripheral parts of the frontoparietal bear bony radial ridges which are most prominent posteriorly.

The dermal sphenethmoid is large and centrally located between the nasals and frontoparietals. The dorsal surface of the bone is completely co-ossified and marked by a pattern of bony ridges, which radiate from the center of the bone. The dorsally exposed dermal sphenethmoid is confluent with the underlying endochondral sphenethmoid as described for *Tripurion petasatus*, *Hyla septentrionalis*, *Osteocephalus taurinus*, and *Trachycephalus nigromaculatus*.

The endochondral sphenethmoid is in synostotic continuity with the septum nasi anteriorly. The sphenethmoid is entirely ossified at the level of the orbitonasal foramen. The structure of the sphenethmoid in sections just posterior to the level of the orbitonasal foramen suggests that some cartilage is present at the distal tip of the anterolateral wing of the sphenethmoid. Just posterior to the terminus of the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. The fontanelle extends posteriorly to approximately the level of the optic foramen. Some cartilage appears in the sphenethmoid near its posterior terminus, but perichondral ossification is always well developed.

The anterior end of the parasphenoid lies at a level posterior to the orbitonasal foramen. The parasphenoid is moderately developed; it lies ventral to the sphenethmoid and prootic. The ventral surface of the parasphenoid bears a long, well developed series of odontoids.

The bursa angularis is well developed and lies in the posterior part of the orbit. The bursa is tubular and lies parallel to the jaw between the maxillary and pterygoid bones. Anteriorly, the gland is a mass of lymphoid tissue. Just anterior to the level of the longitudinal aperture of the bursa connecting the gland with the oral cavity, a central lumen of small diameter appears. The

structure of the bursa is almost identical to that of *Trachycephalus nigromaculatus*.

*The Otic and Occipital Regions.*—In dorsal view the squamosal is a slim bone which extends from the posterior edge of the orbit to the level of the occipital crest. The dorsal and lateral surfaces of the squamosal are spinose and co-ossified. The anterior arm of the squamosal is robust. It does not articulate with the maxillary ventrally, although it lies dorsally adjacent to the maxillary. The posterior arm of the squamosal is equal to length to the anterior arm; it terminates posteroventrally to the posterolateral corner of the frontoparietal. The posterior arm lies laterally adjacent to the frontoparietal; ventral to the frontoparietal, the post-squamosal arm articulates with the crista parotica. The ventral arm of the squamosal is moderately robust. It extends posteroventrally from the mid-point of the arc formed by the anterior and posterior arms of the squamosal and articulates with the pterygoid and quadratojugal ventrally.

The pterygoid is robust. The anterior end of the anterior ramus extends posteriorly adjacent to the maxillary. At a level anterior to the posterior end of the pars dentalis of the maxillary, the pterygoid diverges medially from the maxillary. The posterior ramus of the pterygoid articulates with the ventral arm of the squamosal. The medial ramus is strong and articulates firmly with the prootic.

The quadratojugal is well developed. The anterior end lies medially, adjacent to the maxillary, at a level slightly anterior to the oculomotor foramen. The quadratojugal increases in size posteriorly, whereas the maxillary gradually diminishes in size. Posteriorly, the ossification of the quadratojugal invades the cartilage of the quadrate process.

The trochlear foramen lies dorsally adjacent to the lamina perpendicularis of the frontoparietal and within the bony margins of the optic foramen. The trochlear and optic nerves are separated by connective tissue. The oculomotor foramen lies posteroventral to the optic foramen, and is only narrowly separated from the posterodorsal prootic foramen. There are two acoustic foramina. The jugular foramen lies a short distance posterior to the posterior acoustic foramen. The otic and occipital regions of *T. jordani* are doubtless very well ossified. The specimen utilized for the description of the internal morphology, olfactory, otic and occipital regions is immature; thus, definitive treatment of the morphology of these areas must be postponed until suitable material is available for study.

The pseudobasal and otic processes appear at the anterior level of the oculomotor foramen. In posterior sections, the otic process expands greatly in size and fuses ventrally with the pseudobasal process at the anterior level of the prootic foramen. In subsequent sections, at the level of the prootic foramen, the otic process joins the otic capsule medially, forming the crista parotica, and diverges ventrally from the pseudobasal process. A short distance posterior to the prootic foramen, the pseudobasal process joins the ventral part of the otic capsule medially.

The pars ascendens plectri, pars externa plectri, and distal part of the pars media plectri lie slightly anterior to the level of the anterior acoustic foramen. The medial parts of the pars media plectri and the pars externa plectri lie at the level of the anterior acoustic foramen. The anterior end of the operculum lies between the levels of the two acoustic foramina. The operculum increases in

size in posterior sections, and at the level of the posterior acoustic foramen has replaced the pars interna plectri and closed the foramen ovale. The operculum terminates anterior to the level of the jugular foramen.

*The Articular Region.*—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenial bone. Posteriorly, the cartilage assumes a position dorsal to the angulosplenial bone and then enlarges and comes to lie in close association with the posterior ramus of the pterygoid, the ventral arm of the squamosal, and the quadrate process. The quadratojugal ossification invades the cartilage of the quadrate process at a level just anterior to the posterior acoustic foramen. The intrusive ossification and quadratojugal terminate a short distance posterior to the posterior acoustic foramen. At this level, the posterior terminus of the ventral arm of the squamosal and the posterior ramus of the pterygoid flank the quadrate process dorsolaterally and dorsomedially, respectively. Meckel's cartilage lies ventral to the quadrate process and is underlain by the arcuate angulosplenial bone.

### Cranial Morphology of *Corythomantis greeningi*

The skull of *Corythomantis* is longer than wide (Pl. 8a, b). The snout, in dorsal view, is moderately narrow, but rounded terminally. The dorsal surfaces of the skull are involved in integumentary-cranial co-ossification. The development of co-ossified tissue varies on the dorsal surface of the cranium. Skin overlying dorsolateral parts of the skull is typical of co-ossified tissue; it has a thin epidermal layer which is underlain by loose connective tissue, and it lacks a lower, dense connective tissue layer. Skin overlying dorsomedial parts of the skull is histologically transitional between normal and co-ossified tissue. Some dense connective tissue occurs in the dermis; it is irregular in thickness, poorly organized, and separated from the underlying dermal bones. Dorsally, all dermal bones are sculpted in a pattern of low, reticulate ridges (Pl. 8a). The distal margins of dermal roofing bones and the squamosals and maxillary terminate in spinose protuberances. The skull of *Corythomantis* is characterized by the presence of a dermal sphenethmoid, an extremely reduced quadratojugal, and extensive nasals. The prenasal and palatine bones are absent, and the parasphenoid is poorly developed. The vocal sac is single, median, and subgular.

*The Olfactory Region.*—The premaxillaries (Pl. 8b) are small and lie posterior to the anterior ends of the nasals and maxillaries. The lateral corner of the pars dentalis of the premaxillary is covered by the maxillary and the anterior surface of the alary process of the premaxillary is covered by the nasal. The rest of the bone is externally exposed and not involved in integumentary-cranial co-ossification. The premaxillaries are separated medially from one another and laterally from the maxillaries by dense connective tissue. Ventromedially, each premaxillary bears a small, inconspicuous palatine process. The alary process of the premaxillary is anterodorsally oriented and about one and one-half times as long as the depth of the pars dentalis of the premaxillary. The process is slightly convex anteriorly and in contact with the superior prenasal cartilage dorsally.

In ventral view (Pl. 8b) the prevomer lies lateral to the midline of the skull and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer is associated with the ventrolateral surface of the solum nasi dorsal to

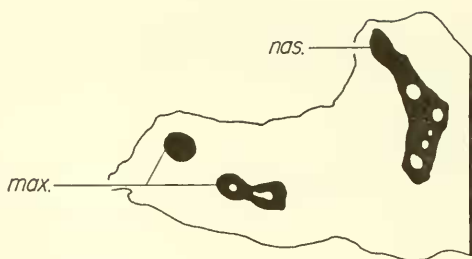
the pars palatina and pars dentalis of the maxillary and premaxillary; the prevomer is separated from the latter bones by dense connective tissue. The prevomer bears delicate anterolateral and posterolateral processes which form the anterior, medial, and posterior margins of the internal nares. The denticulous processes of the prevomer are small and oriented at a slight angle (see Table 1) to the midline of the skull. Posteriorly the prevomer provides bony support for the olfactory eminence and articulates with the sphenethmoid.

The nasals (Pl. 8a) are extremely large. Anteriorly, the nasal terminates in spinose protuberances at the tip of the snout anteromedial to the maxillaries and premaxillaries. The nasals converge medially from their anterior termini posterior to the anterior tip of the dermal sphenethmoid. The ventrolateral margin of the nasal articulates with the pars facialis of the maxillary except where the former forms the anterior, medial, and posterior margins of the external nares. Posterolaterally, the nasal forms the bony anterior margin of the orbit. The posterior margin of the nasal articulates with the frontoparietal and the posteromedial margin with the dermal sphenethmoid. The dorsal surface of the nasal is completely involved in integumentary-cranial co-ossification. The nasal bears a moderately developed canthal ridge. The ridge extends from the anterodorsal corner of the orbit to the tip of the snout and is best developed anteriorly. The entire surface of the nasal is marked by a reticulate network of low bony ridges. The orbital margin of the nasal terminates in a slight, upturned flange bearing small, denticulate spines.

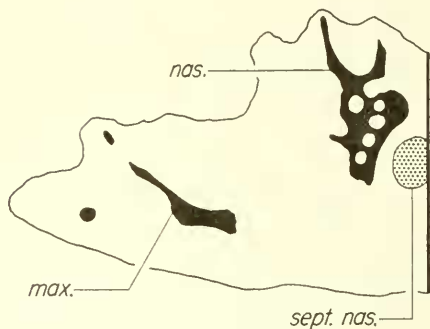
The maxillary is moderately robust. Anterior to the orbit the maxillary bears a shallow flange of spinose protuberances which decrease greatly in size ventral and posterior to the orbit. The dorsal surface of the maxillary is involved in integumentary-cranial co-ossification and is marked by a reticulate network of low, bony ridges. Medially, the maxillary bears a pars palatina dorsal to the pars dentalis. The pars palatina is best developed anterior to the orbit; ventral to the orbit, the pars palatina is barely evident. Dorsal to the pars palatina and anterior to the orbit, the maxillary bears a moderately developed pars facialis. The latter articulates with the nasal except where it forms the ventral margin to the external nares. Posteriorly, the pars facialis terminates at the anterior margin of the orbit which is formed by the nasal. The maxillary is exceptionally long; it terminates posteriorly adjacent to the posteroventral terminus of the ventral arm of the squamosal.

The anterior end of the septum nasi appears between the nasals anterior to the alary processes of the premaxillary (Figs. 62-63). The tectum nasi appears dorsolateral to the septum at the anterior end of the alary process, in subsequent sections, the septum nasi and tectum nasi fuse. A short distance posterior to the appearance of the tectum, the superior prenasal cartilage is present on the posterodorsal face of the alary cartilage (Fig. 64); the prenasal cartilage is joined laterally to the alary cartilage. The anterior end of the cavum principale lies anterior to the level of the pars dentalis of the premaxillary; the cavum (Fig. 64) is encased by the septum nasi and tectum nasi laterally and the alary cartilage laterally and ventrally. The superior prenasal cartilage fuses with the solum nasi at the level of the anterior margin of the external nares. Just posterior to the latter level, the anterior end of the cavum medium appears ventral to the cavum principale and septomaxillary. At the same level, the cartilago obliquus appears along the posteromedial surface of the alary process of

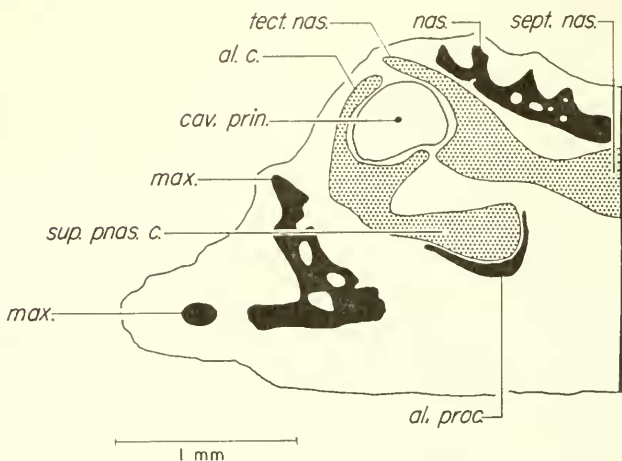
62



63



64



FIGS. 62-64. Transverse sections through the anterior end of the skull of *Corythomantis greeningi* (KU 92222): (62) anterior level of nasal and maxillary; (63) anterior level of septum nasi; (64) level of cavum principale and alary process of premaxillary. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *cav. prin.*, cavum principale; *max.*, maxillary; *nas.*, nasal; *sept. nas.*, septum nasi; *sup. pnas. c.*, superior prenasal cartilage; *tect. nas.*, tectum nasi.

the premaxillary. The anterior end of the cavum inferius lies in the lateral part of the solum nasi at the level of the pars dentalis of the premaxillary. The crista subnasalis is absent. The septum nasi is ossified at the anterior level of the olfactory eminence. Ossification of the solum nasi occurs at the level of the internal naris.

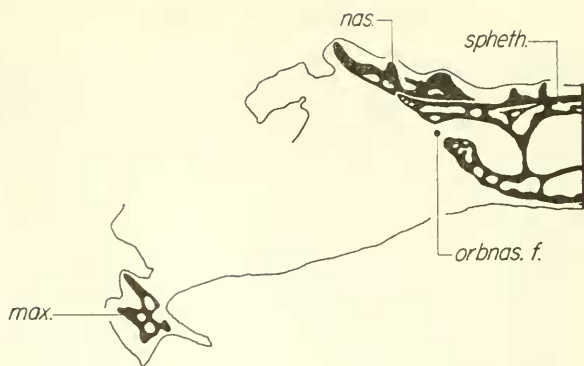
The anterior end of the septomaxillary is a delicate, arcuate-shaped bone which is horizontally oriented and lies ventrolateral to the cavum principale at the anterior level of the external naris. The anterior ramus increases in size and bifurcates medially to accommodate the lateral part of the cavum medium. In posterior sections, a slim, dorsal ramus appears. At the same level, the ventral part of the septomaxillary diverges from the anterior ramus, the latter being separated from the former by the cavum medium. The anterior ramus bifurcates into medial and lateral rami at the level of the appearance of the dorsal ramus. Posterior to the divergence of the nasolacrimal duct from the cavum medium, the ventral ramus of the septomaxillary fuses with the robust dorsal and lateral rami.

*The Sphenethmoid and Orbital Region.*—The frontoparietals (Pl. 8a) converge medially throughout their lengths. Anteriorly the frontoparietal articulates with the nasal; anteromedially, the frontoparietal articulates with the posterior margin of the dermal sphenethmoid. Anterolaterally, the frontoparietal extends over the orbit as a narrow shelf. The posterior margin terminates in a small, upturned, spinose occipital crest. Ventral to the crest, the frontoparietal is attached to the exoccipital; laterally, it bridges the prootic from the exoccipital to the posterior arm of the squamosal. The entire dorsal surface of the frontoparietal is involved in integumentary-cranial co-ossification. The outer margins of the bone are marked by series of small, denticulate spines; the rest of the dorsal surfaces are covered by a fine reticulate network of bony ridges.

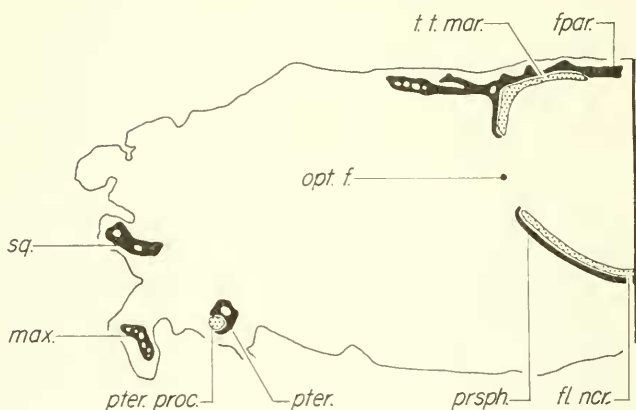
The dermal sphenethmoid (Pl. 8a) is a triangular-shaped bone centrally located at the anterior level of the orbit; the bone lies posteromedial to the nasals and anteromedial to the frontoparietals. The dermal sphenethmoid is completely involved in integumentary-cranial co-ossification and the dorsal surface of the bone is marked by a reticulate network of bony ridges. The dorsally exposed dermal sphenethmoid is confluent with the underlying endochondral sphenethmoid as is described for *Triprion petasatus* and *Hyla septentrionalis*.

Anteriorly the endochondral sphenethmoid is in synosteotic continuity with the septum nasi. It is separated from the overlying nasals and frontoparietals by a thin layer of dense connective tissue. Posterior to the planum, the sphenethmoid is completely bony; the margins of the orbitonasal foramen are bony (Fig. 65). Cartilage appears at the distal tip of the anterolateral wing of the sphenethmoid at the level of the articulation of the frontoparietal and nasal. The cartilage expands distally to form a broad supraorbital shelf. The supraorbital cartilage extends, from the sphenethmoid, ventral to the frontoparietal, laterally over the dorsal surface of the eye. The cartilage gradually diminishes in size in posterior sections. Just posterior to the terminus of the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. The fontanelle extends posteriorly to the level of the optic foramen. At the latter level, the posterior margin of the fontanelle is formed by the tectum synoticum. A second area of cartilage is

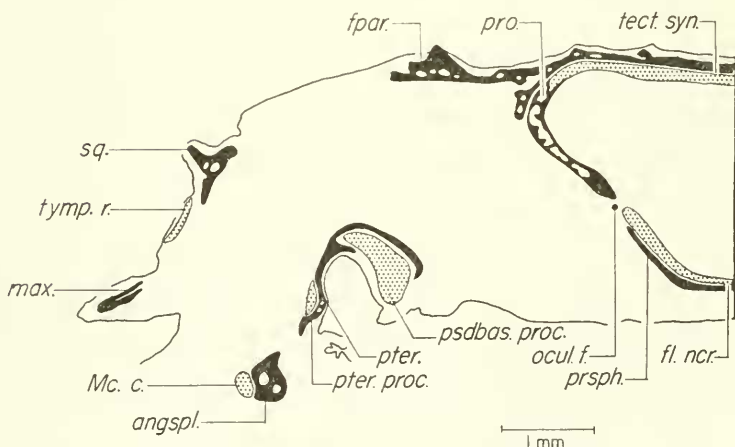
65



66



67



FIGS. 65-67. Transverse sections through the skull of *Corythomantis greeningi* (KU 92222) at levels of cranial nerve foramina: (65) level of orbitonasal foramen; (66) level of optic foramen; (67) level of oculomotor foramen. Abbreviations: *angsp.*, angulospl. process; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *nas.*, nasal; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *orbnas. f.*, orbitonasal foramen; *pro.*, prootic; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *spheth.*, sphenethmoid; *sq.*, squamosal; *t. t. mar.*, tectum tecti marginalis; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

found in the sphenethmoid at the posterior level of the orbit. The cartilage appears as the taenia tecta marginalis forming the lateral margins of the frontoparietal fontanelle. In subsequent sections, the amount of cartilage present increases; at a level anterior to the optic foramen, the entire sphenethmoid is cartilaginous.

The anterior end of the parasphenoid (Pl. 8b) lies at a level just posterior to the trochlear foramen. The parasphenoid is extremely thin and poorly developed; it lies ventral to the sphenethmoid and prootic and forms a weak bridge of support for the cartilaginous neurocranial floor. The parasphenoid is separated from adjacent bones by an exceedingly thin layer of connective tissue which is better developed anteriorly than posteriorly. The ventral surface of the parasphenoid is smooth and does not bear any odontoid structures.

The bursa angularis oris is very well developed and lies in the posterior part of the orbit. The bursa is tube-shaped and lies parallel to the jaw between the maxillary and pterygoid bones. The gland consists of a mass of lymphoid tissue loosely encased in connective tissue. The bursa is closed at the anterior and posterior ends but it bears a central lumen which lies parallel to the length of the gland. At approximately the mid-length of the bursa, the central lumen opens to the mouth.

*The Otic and Occipital Regions.*—In dorsal view (Pl. 8a), the squamosal is an arcuate bone which extends posteriorly from the posterior edge of the orbit to the level of the occipital crest. The dorsolateral margin of the squamosal bears a series of small, denticulate spines and is involved in integumentary-cranial co-ossification. The anterior arm of the squamosal is moderately robust. It forms part of the posterior margin of the orbit and terminates ventrally on the dorsal surface of the maxillary. The articulation of the anterior arm of the squamosal on the maxillary is loose; the two bones are separated by dense connective tissue. The posterior arm of the squamosal is shorter than the anterior arm; the former terminates at the posterolateral corner of the frontoparietal. The posterior arm articulates medially with the frontoparietal or is separated from the latter by connective tissue. The ventral arm of the squamosal extends posteroventrally from the mid-point of the arc formed by the anterior and posterior arms of the squamosal; posteroventrally, the terminus lies dorsal to the quadrate process between the posterior ramus of the pterygoid and the posterior end of the maxillary.

The pterygoid is well developed (Pl. 8b). The anterior end of the anterior ramus lies at a level just posterior to that of the orbitonasal foramen. The anterior ramus extends posteriorly adjacent to the maxillary and posterior maxillary process. At a level slightly anterior to the posterior end of the pars dentalis of the maxillary, the pterygoid and pterygoid process diverge medially from the maxillary. The posterior ramus articulates with the quadrate process and ventral arm of the squamosal. The medial ramus is strong and articulates firmly with the ventral ledge of the otic capsule.

The quadratojugal is small and poorly developed. The anterior end (Fig. 68) lies midway between the levels of the prootic foramen and anterior acoustic foramen. Anteriorly, the quadratojugal is a small rod of bone lying medial to the maxillary and separated from the latter by an extensive layer of dense connective tissue. In subsequent posterior sections, the bone increases slightly in size and becomes involved in ossification of the quadrate process at the

anterior level of the posterior acoustic foramen. The posterior terminus of the quadratojugal lies at the mid-level of the posterior acoustic foramen.

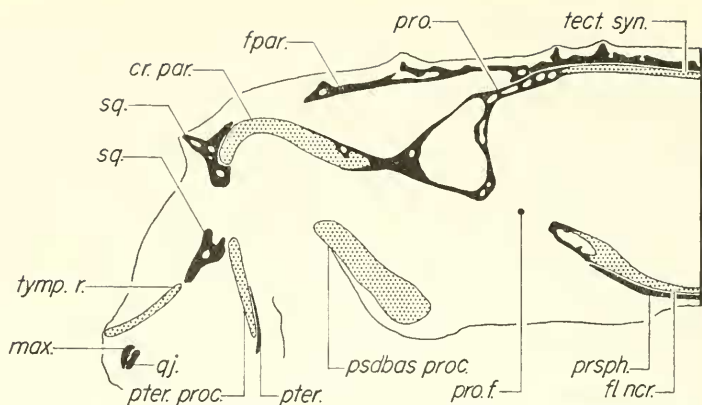
The anterior, dorsal, and ventral margins of the optic foramen (Fig. 66) are bony and formed by the lamina perpendicularis dorsally and the parasphenoid ventrally; posteriorly the bony margin of the foramen is formed by the prootic. The trochlear foramen lies dorsally adjacent to the prootic in the posterodorsal part of the optic foramen. The optic and trochlear foramina are separated by connective tissue. The oculomotor foramen (Fig. 67) lies posterior and slightly ventral to the optic foramen. The margins of the oculomotor foramen are bony. The prootic foramen (Fig. 68) lies immediately posterior and slightly dorsal to the oculomotor foramen. The margins of the prootic foramen are bony. There are two acoustic foramina. The anterior acoustic foramen (Fig. 69) lies at the level of the pars media plectri and is bordered by bone. The anterodorsal margin of the posterior acoustic foramen (Fig. 70) lying at the level of the pars interna plectri and anterior end of the operculum, is cartilaginous, whereas the ventral and posterior margins of the foramen are bony. The margins of the jugular foramen, posteriorly, are bony.

The pseudobasal process (Fig. 67) appears at the anterior level of the prootic foramen. The process lies lateral to the neurocranium and slightly posterior to its appearance, the pseudobasal process expands dorsolaterally into the otic process. The otic process lies medially adjacent to the anterior arm of the squamosal. For a short distance, the otic process is continuous with the pseudobasal process ventromedially and the pterygoid process ventrolaterally. The otic process diverges from the pseudobasal process at the mid-level of the prootic foramen. At a slightly posterior level, the otic process is separated from the pterygoid process by the squamosal; at the same level, the otic process joins the otic capsule medially to form the crista parotica (Fig. 68). Just posterior to the latter fusion, the cornu principalis of the hyale diverges laterally from the pseudobasal process.

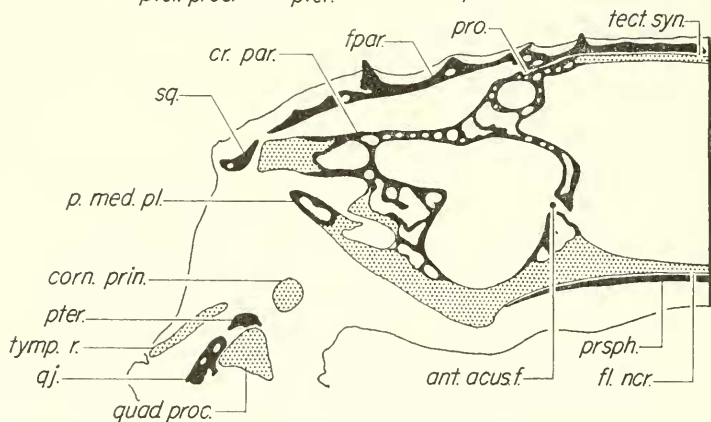
The pars externa and pars ascendens plectri are cartilaginous and appear just anterior to the level of the anterior acoustic foramen. At the level of the anterior acoustic foramen and the fusion of the pars ascendens and pars externa plectri, the pars media plectri appears distally, fused to the dorsum of the pars externa plectri. Laterally, the pars media plectri is cartilaginous; medially, it is bony. In subsequent sections, the bony pars media plectri moves medially; at the anterior margin of the posterior acoustic foramen, the pars media plectri fuses with the lateral edge of the otic capsule. The pars interna plectri is cartilaginous and lies posteromedial to the pars media plectri. The cartilaginous operculum appears just posterior, at the mid-level of the posterior acoustic foramen (Fig. 70) and terminates posterior to the posterior acoustic foramen.

At the posterior level of the optic foramen, the prootic is ossified only peripherally at the margins of the foramen; the floor and roof of the neurocranium are cartilaginous. In posterior sections, ossification progresses from the level of the optic foramen dorsomedially in the neurocranium. At the level of the prootic foramen, the sides of the braincase are ossified, but the floor of the neurocranium and the tectum synoticum dorsally are cartilaginous. The tectum synoticum is cartilaginous throughout its length, whereas a moderate invasion of bone occurs in the neurocranial floor. At the terminus of the cranium, the ventromedial part of the neurocranial floor is cartilaginous. The pars externa plectri,

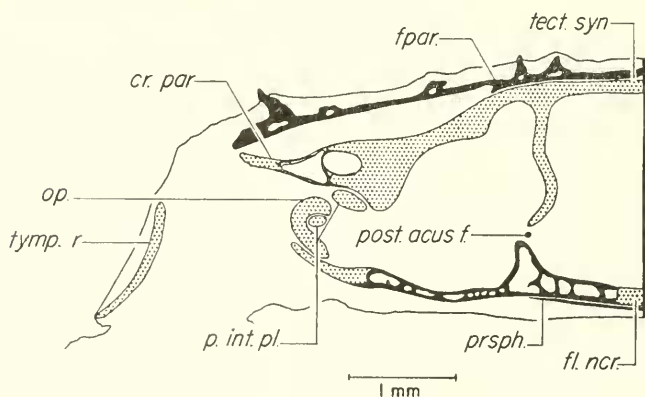
68



69



70



FIGS. 68-70. Transverse sections through the skull of *Corythomantis greeningi* (KU 92222) at levels of cranial nerve foramina: (68) level of prootic foramen; (69) level of anterior acoustic foramen; (70) level of posterior acoustic foramen. Abbreviations: ant. acus. f., anterior acoustic foramen; corn. prin., cornu principalis; cr. par., crista parotica; fl. ncr., floor of neurocranium; fpar., frontoparietal; max., maxillary; op., operculum; p. int. pl., pars interna plectri; p. med. pl., pars media plectri; post. acus. f., posterior acoustic foramen; pro., prootic; pro. f., prootic foramen; prsph., parasphenoid; psdbas. proc., pseudo-basiprocess; pter., pterygoid; pter. proc., pterygoid process; qj., quadrate process; quad. proc., quadrate process; sq., squamosal; tect. syn., tectum synoticum; tymp. r., tympanic ring.

pars ascendens plectri, pars interna plectri, and operculum are cartilaginous. The distal and medial tips of the pars media plectri are cartilaginous; centrally, the bone is well ossified. The distal part of the crista parotica, adjacent to the squamosal, is cartilaginous; medially, the crista parotica and the dorsal part of the otic capsule are ossified, whereas the otic capsule floor is cartilaginous. Posteriorly, ossification decreases in dorsal parts of the otic capsule and increases in ventral parts. At the level of the posterior acoustic foramen, only the distal tip and part of the floor of the otic capsule are ossified. At the level of the jugular foramen, the skull is bony with the exceptions of the dorso- and ventromedial parts of the braincase and the posterodorsal part of the otic capsule.

*The Articular Region.*—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenial bone. Posteriorly, the cartilage assumes a position dorsal to the angulosplenial bone and then enlarges and comes to lie in close association with the posterior ramus of the pterygoid, the ventral arm of the squamosal, and the quadrate process at the posterior level of the pars media plectri. At the level of the posterior acoustic foramen, the ossification of the quadratojugal invades the cartilage of the quadrate process. The quadratojugal, maxillary, and posterior ramus of the pterygoid terminate at the posterior margin of the posterior acoustic foramen. At a slightly posterior level the squamosal terminates; the disappearance of the latter is followed by the termination of the quadrate process. Meckel's cartilage persists a short distance posteriorly.

*Remarks.*—The only variation noted among three males of *Corythomantis greeningi* was in the posterior development of the frontoparietal. The smallest specimen (11.2 mm. head length) shows the least development of this bone. The posterior margin of the frontoparietal bears no occipital crest and does not articulate with the bony part of the exoccipital. Posterolaterally, the frontoparietal bears a flange which extends over the anteromedial part of the crista parotica but does not articulate with the squamosal. A slightly larger individual (13.3 mm. head length) has a better developed frontoparietal. The frontoparietal articulates with the exoccipital posteriorly, but does not terminate in an upturned flange; lateral development of the frontoparietal is unchanged from the condition of the smaller specimen. The third specimen (head length 14.1 mm.) is fully developed.

The skull of *Corythomantis greeningi* bears a clear resemblance to a species (Fig. 71a) known from Jacareacanga, Pará Province, Brazil (represented by specimens in the collections of the University of Kansas and of Werner C. A. Bokerman, São Paulo, Brazil), which is an undescribed member of the species complex called *Hyla rubra*. The skull of this species differs from that of *Hyla rubra* (Fig. 71b) from Jacareacanga in the following aspects: the skull is longer in proportion to its width than in *H. rubra*; the sphenethmoid is rounded anteriorly, whereas it is truncate in *H. rubra*; the anterior arm of the squamosal articulates with the maxillary, whereas in *H. rubra* it does not; and the parasphenoid is poorly developed.

Comparison of plate 8a and figure 71a shows the similarity of *Corythomantis greeningi* to this unnamed species of the *Hyla rubra* group. The shapes and proportions of the two skulls resemble one another. Both have extensive squamosals, poorly developed parasphenoids, and pterygoids having medial

rami which articulate with the prootic. There is a poorly developed palatine in the unnamed species and no palatine in *C. greeningi*. Internally, the cranial structures of these species resemble one another in general pattern, and notable similarities occur in the structure of the septomaxillary and the bursa angularis oris. The primary difference noted in internal structure is the presence of the crista subnasalis in the unnamed species. Externally, this species resembles *Hyla rubra* in size, character of the feet and general appearance. Osteologically, the long, narrow skull has a small prootic region and extremely large nasals; these characters relate this frog to the *Hyla rubra* group.

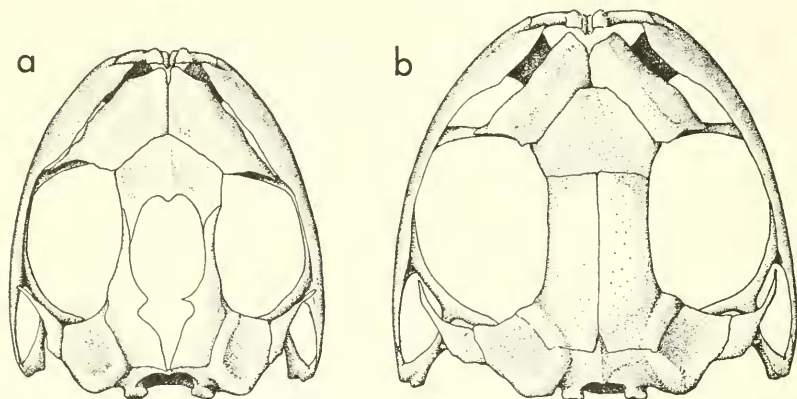


FIG. 71. Dorsal views of skulls of *Hyla rubra*,  $\times 4.5$ : (a) KU 92151 from Jacareacanga, Para, Brazil; (b) KU 104411 from Santa Cecilia, Napo, Ecuador.

### Cranial Morphology of *Aparasphenodon brunoi*

The skull of *Aparasphenodon brunoi* is longer than wide (Pl. 9a). The snout, in dorsal view, is narrow and acuminate. All dorsal surfaces of the skull are involved in integumentary-cranial co-ossification. Dorsally, all dermal bones are sculptured in patterns of pronounced parallel ridges. The termination of these ridges at the distal margins of all dermal bones results in delicate series of extremely small spinules. The latter are best developed on the outer edge of the maxillary, the canthal ridge near the orbit, on the nasal and frontoparietal at the margin of the orbit and at the posterior edge of the frontoparietals. *Aparasphenodon* lacks a well developed occipital crest. The skull of *Aparasphenodon* is characterized by an acuminate snout; the presence of a dermal sphenethmoid and prenasal, a moderate labial flange on the maxillary, angled vomerine teeth (see Table 1), and the presence of a prominent anteroventral crest on the base of the parasphenoid. The vocal sac is single, median, and subgular.

*The Olfactory Region.*—The prenasal (Pl. 9a) lies anterior to the premaxillaries and nasals and between the anterior ends of the maxillaries. The bone is flat ventrally; dorsally, it bears a broad medial ridge marked with longitudinal, parallel ridges. The anterior tip of the prenasal bears a group of short spines. The prenasal lacks a labial flange. Posterolaterally, the prenasal articulates with the maxillary; posteromedially, it articulates with the anterior margins of the

nasals, except where it forms the anterior margin of the external nares. Ventrally, the prenasal is not co-ossified. It articulates posterolaterally with the labial flanges of the maxillaries. The ventromedial margin of the prenasal is free and lies anterior to the medial articulation of the premaxillaries. Internally, the anterior end of the prenasal contains many small cavities. A short distance posterior to the anterior end a single, central cavity appears which houses the anterior end of the septum nasi. In subsequent sections, the anterolateral corners of the tectum nasi appear laterally, adjacent to the prenasal. Slightly posterior, the dorsal and ventral parts of the prenasal split to form the external nares; at this level the external part of the tectum nasi fuses medially with the septum nasi. Posterior to the fusion of the tectum and septum nasi, the prenasal consists of an upper plate of bone overlying the septum and tectum nasi dorsomedially and a lower plate of bone underlying the nasal cartilages and alary processes of the premaxillary. Ventrally, the prenasal is separated from the maxillary by dense connective tissue. Dorsomedially, the prenasal overlaps the nasals posteriorly.

The premaxillaries (Pl. 9b) lie posterior to the prenasal and the anterior ends of the labial flanges of the maxillary. Dense connective tissue separates the maxillary from the anterolateral edges and lateral corners of the premaxillaries. The premaxillaries are narrowly separated medially by connective tissue. A small, inconspicuous palatine process is present posteromedially on the premaxillary. The alary process of the premaxillary is long, dorsally concave, and inclined anteriorly at approximately a 45-degree angle. The process is straight and lies just dorsal to the ventral plate of the prenasal. The anterior end of the alary process lies at the level of the anterior bony margin of the external nares.

In ventral view (Pl. 9b), the prevomer lies lateral to the midline of the skull, and ventral to the solum nasi and sphenethmoid. The anterolateral corner of the prevomer lies dorsal to the pars dentalis of the premaxillary and the labial flange of the maxillary. At the level of the palatine process of the premaxillary, the crista subnasalis diverges from the solum nasi and the prevomer thickens around the lateral edge of the solum to form a robust bony support for the olfactory eminence. The prevomer bears well developed lateral wings that form the anterior and medial margins of the internal nares. The prevomerine dentigerous processes are large and form an angular pattern (see Table 1).

The palatine is a robust bone that lies posterior to the internal naris. The broad, distal end is lodged in connective tissue dorsal to the pars palatina of the maxillary and adjacent to the anterior maxillary process and pars facialis of the maxillary. The proximal end of the palatine lies ventral to the lateral, bony edge of the sphenethmoid and is separated from the sphenethmoid by a thin layer of dense connective tissue. The palatine bears a prominent ridge which terminates ventrally in a series of delicate odontoid spines.

The nasal is extremely large. Anteriorly, this bone articulates with the prenasal except where the former forms the posterior margins of the external naris. Laterally it articulates with the pars facialis of the maxillary and posterolaterally it forms the bony anterior margin of the orbit. The nasals converge anteromedially to the dermal sphenethmoid. The posterior margin of the nasal articulates with the frontoparietal dorsolaterally and the dermal sphenethmoid dorsomedially. The dorsal surface of this bone is completely involved in integumentary-cranial co-ossification. It bears a well developed canthal ridge extend-

ing from the posteromedial edge of the external naris to the anterodorsal corner of the orbit, where a series of small, deep pits appear in the ridge. A series of prominent ridges radiate out over the surface of the nasal from the posterior crest of the ridge. The ridges are best developed along the crest of the ridge and on the dorsal surface of the nasal.

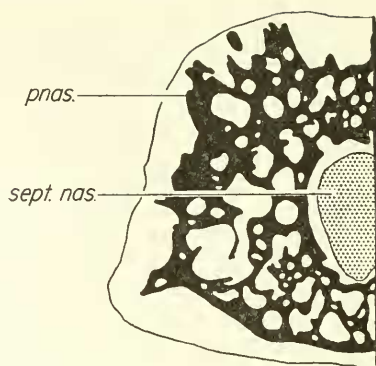
The maxillary is moderately robust and bears a relatively narrow flange which is most evident in ventral and lateral views. The flange is most extensive anterior to the premaxillaries. At this level and for a short distance posteriorly, the flange is horizontally oriented. At a level slightly anterior to the orbit, the maxillary flange diminishes in size and gradually assumes a more nearly vertical orientation lateral to the pars dentalis of the maxillary. The dorsal surface of the maxillary is involved in integumentary-cranial co-ossification; the ventral and lateral surfaces are not co-ossified. The pars facialis and pars palatina are well developed anteriorly; they diminish in size ventral to the orbit. The maxillary terminates posteriorly on the outer edge of the quadratojugal.

The anterior end of the nasal capsul lies far forward in the cranium, just posterior to the anterior end of the prenasal. The cartilaginous septum nasi projects anteriorly into a small medial cavity in the anterior tip of the prenasal (Fig. 72). The anterior corners of the tectum nasi exterior to the prenasal (Fig. 73), fusing with the septum a short distance posterior at the anterior margin of the external nares (Fig. 74). At a level just anterior to the fusion of the tectum and septum, the alary cartilage and superior prenasal cartilage appear ventral to the tectum, associated with the anterior tip of the alary process of the premaxillary. The lateral expansion of the solum separates the alary cartilage from the superior prenasal cartilage; the latter terminates at the level of the anterior end of the cavum medium. The inferior prenasal cartilage appears on the dorsomedial face of the alary process at the anterior ends of the recessus medialis and recessus lateralis of the cavum inferius; the inferior prenasal cartilage fuses with the solum posteriorly at a level just anterior to the formation of the planum terminale. A short crista subnasalis is present at the level of the palatine process of the premaxillary. The septum nasi is partly ossified at the anterior margin of the internal nares. At this level, cartilaginous lateral remnants of the solum are present in the olfactory eminence; the ventromedial part of the solum has been replaced by the prevomer. In posterior sections, at the mid-level of the internal nares, all cartilage is replaced by bone except the anterior maxillary process.

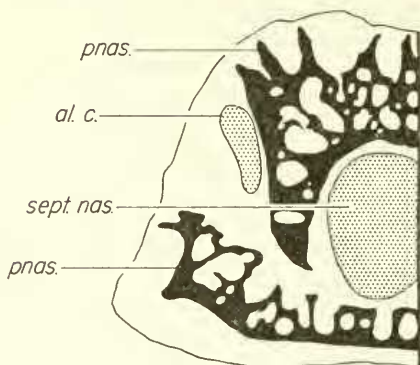
The anterior end of the septomaxillary is a horizontally oriented bar of bone, lying ventrolateral to the cavum principale at the mid-level of the external naris. The bone thickens laterally around the lateral edge of the cavum medium. As the cavum enlarges, it comes to lie within the septomaxillary. In cross-section, the latter resembles a "U" lying on its side with the open end facing ventromedially. In slightly posterior sections, the ventral side diverges from the main body of the U as the ventral ramus of the septomaxillary; the remaining dorsal part of the septomaxillary develops a vertically oriented dorsal ramus and then bifurcates into medial and lateral rami. The dorsal ramus is associated with the lateral septomaxillary ramus. Posterior to the lateral divergence of the nasolacrimal duct from the cavum medium, the ventral ramus of the septomaxillary fuses with the dorsolateral ramus.

*The Sphenethmoid and Orbital Regions.*—The frontoparietal articulates

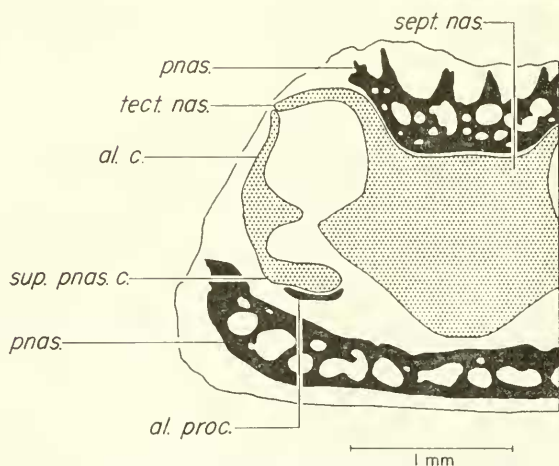
72



73



74



FIGS. 72-74. Transverse sections through the anterior end of the skull of *Aparasphenodon brunoï* (KU 92214): (72) level of prenasal and anterior end of septum nasi; (73) anterior level of tectum nasi; (74) anterior level of alary cartilage and alary process of premaxillary. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *pnas.*, prenasal; *sept. nas.*, septum nasi; *sup. pnas. c.*, superior prenasal cartilage; *tect. nas.*, tectum nasi.

anterolaterally with the nasal and anteromedially with the dermal sphenethmoid (Pl. 9a). It forms a broad, bony supraorbital shelf and articulates posterolaterally with the squamosal. The frontoparietals converge medially throughout their entire lengths. The posterior margin of the frontoparietal overhangs the exoccipital medially, and laterally bridges the prootic to the squamosal. The dorsal surface of the frontoparietal is involved in integumentary-cranial co-ossification. The central part of the frontoparietal is pitted and rugose. From this area, ridges radiate out to all margins of the bone.

The dermal sphenethmoid is roughly triangular in shape, the base of the triangle being arcuate rather than flat. The bone lies posteromedial to the nasals and anteromedial to the frontoparietals. The dorsal surface of the dermal sphenethmoid is completely co-ossified and, like the frontoparietal, bears a central rugose area with a radiation of ridges peripherally. The dorsally exposed sphenethmoid is confluent with the underlying endochondral sphenethmoid as described in *Tripurion petasatus*, *Hyla septentrionalis*, and *Corythomantis greeningi*.

The endochondral sphenethmoid is in synosteotic continuity with the septum nasi anteriorly and is separated from overlying nasals and frontoparietals by a thin layer of dense connective tissue. Posterior to the planum antorbitale a small amount of cartilage remains in the dorsolateral corners of the sphenethmoid which lie ventral to the posterodorsal crests of the canthal ridges. This cartilage persists at the distal tip of the anterolateral wing of the sphenethmoid underlying the bony supraorbital shelf of the nasal and the anterior part of the frontoparietal. The margins of the orbitonasal foramen are bony (Fig. 75). Posterior to the terminus of the dermal sphenethmoid, the roof of the endochondral sphenethmoid splits to form the frontoparietal fontanelle ventral to the frontoparietals. Anteriorly, the margins of the fontanelle are bony; posteriorly, at about the mid-level of the orbit, the dorsolateral parts of the sphenethmoid are only partly ossified. From this level, posterior to the terminus of the sphenethmoid at the optic foramen, ossification decreases, and the margins of the frontoparietal fontanelle are formed by the cartilaginous taenia tecta marginalis.

The anterior end of the parasphenoid (Pl. 9b) lies at a level near the posterior end of the dermal sphenethmoid. Anterior to the otic capsule, the parasphenoid is extremely delicate and narrowly separated from the sphenethmoid and prootic dorsally. Posteriorly, at the anterior level of the otic capsule, the parasphenoid develops an unusual, conspicuously thickened, bony, ventral ridge which is transversely oriented. The ridge terminates laterally in thin, ventral projections which face anteroventral knob-like projections of the otic capsule. In sections posterior to this ridge, the parasphenoid becomes thinner and gradually narrows to a terminal point. The ventral surface of the parasphenoid does not bear any odontoid structures.

A bursa angularis oris is present in the posterior part of the orbit. The position and organization of the gland closely resembles that described for *Corythomantis greeningi*.

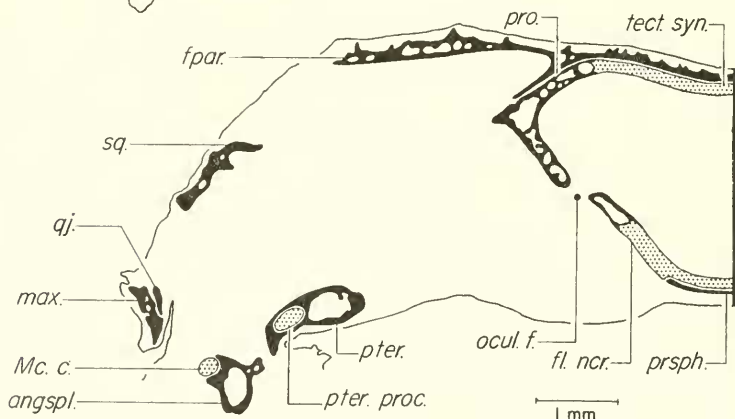
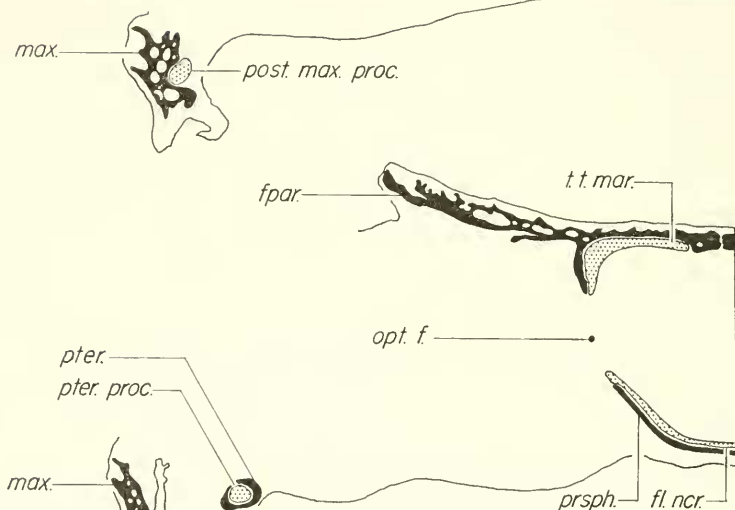
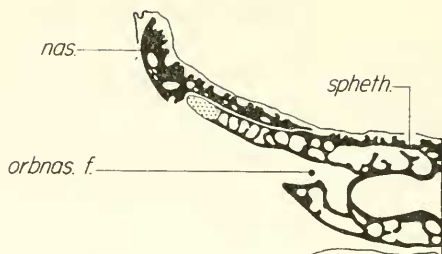
*The Otic and Occipital Regions.*—In dorsal view (Pl. 9a), the squamosal is a long, slim bone which extends from the posterior part of the orbit posteriorly to a level slightly beyond the posterior edge of the frontoparietal. The dorsal surface of the squamosal is co-ossified. The anterior arm of the squamosal is

robust, laterally compressed, and extends slightly more than two-thirds the distance from the junction of the ventral and anterior arms of the squamosal to the maxillary. The posterior arm of the squamosal is equally as robust as the anterior arm but slightly shorter. The posterior arm lies adjacent to the postero-lateral part of the frontoparietal but does not articulate with it. Ventral to the frontoparietal, the posterior arm of the squamosal bears a medial flange which articulates with the dorsolateral edge of the crista parotica. The ventral arm extends posteroventrally from approximately the midpoint of the arc formed by the anterior and posterior arms of the squamosal; posteroventrally, the terminus lies between the posterior ramus of the pterygoid and the quadratojugal.

The pterygoid is well developed (Pl. 9b). The anterior terminus of the anterior ramus of the pterygoid lies dorsal to the pars dentalis of the maxillary and medially adjacent to the posterior maxillary process in the anterior part of the orbit. The posterior ramus articulates with the ventral arm of the squamosal and the quadrate process posteriorly. The medial ramus is in contact with the prootic but does not bear a firm, bony articulation with it.

The quadratojugal lies along the medial surface of the posterior part of the maxillary. The anterior end lies at the posterior level of the optic foramen. The maxillary terminates posteriorly at the anterior level of the acoustic foramen. The quadratojugal terminates posteriorly on the quadrate process. The anterior border of the optic foramen (Fig. 76) is cartilaginous; the lamina perpendicularis of the frontoparietal forms the bony anterodorsal margin and the parasphenoid the anteroventral margin of the foramen. The prootic ossifies to provide the bony posterior margins of the optic foramen. A bridge of bone separates the optic foramen from the more posterior oculomotor foramen (Fig. 77). The margins of the latter are bony. The oculomotor foramen is very narrowly separated by bone from the large prootic foramen (Fig. 78) lying posterior. There is only one acoustic foramen (Fig. 79); it is entirely bordered by bone as is the posterior jugular foramen (Fig. 80).

The pseudobasal process (Fig. 78) first appears posterior to the level of the oculomotor foramen. The anterior tip of the crista parotica (Fig. 78) lies midway between the otic capsule and the squamosal at the mid-level of the prootic foramen. In posterior sections, the crista expands medially to establish a bony connection with the otic capsule and laterally in cartilage to the squamosal. The otic process then diverges ventrally from the crista parotica and fuses first with the pseudobasal process at the level of the posterior margin of the prootic foramen, and then the pterygoid process. At the level of the latter fusion, the ventral ledge of the otic capsule and pseudobasal process fuse. In slightly posterior sections, the otic process terminates, separating the pterygoid process and ventral ledge of the otic capsule from one another and the distal tip of the crista parotica dorsally. Ventrally, the cornu principalis diverges from the ventral, cartilaginous ledge of the otic capsule. The bony medial tip of the pars media plectri appears at the anterior levels of the acoustic foramen and is followed by the pars interna plectri. In posterior sections, the pars media plectri expands laterally toward the pars externa plectri. The latter is connected to the distal tip of the crista parotica by the pars ascendens plectri. The operculum, and the posterior and distal parts of the pars media plectri and pars externa plectri lie at the posterior levels of the acoustic foramen. The operculum terminates posteriorly just anterior to the jugular foramen.



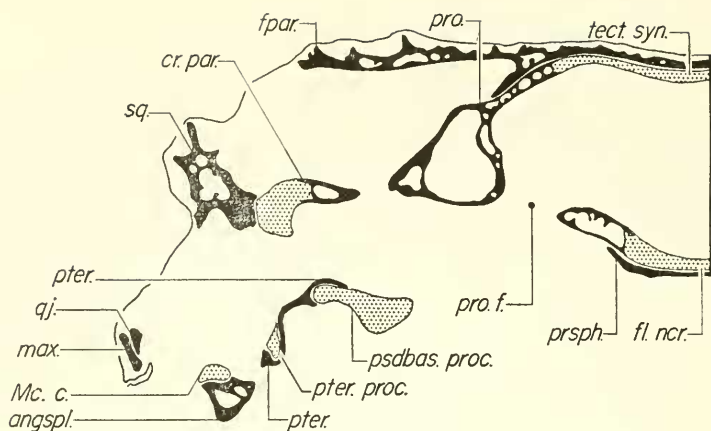
FIGS. 75-77. Transverse sections through the skull of *Aparasphenodon bruni* (KU 92214) at levels of cranial nerve foramina: (75) level of orbitonasal foramen; (76) level of optic foramen; (77) level of oculomotor foramen. Abbreviations: *angsp.*, angulosplenial; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *nas.*, nasal; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *orbnas. f.*, orbitonasal foramen; *post. max. proc.*, posterior maxillary process; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *spheth.*, sphenethmoid; *sq.*, squamosal; *t. t. mar.*, taenia tecti marginalis; *tect. syn.*, tectum synoticum.

At the posterior level of the optic foramen, the prootic is sparsely ossified around the margins of the foramen. The trochlear foramen lies dorsally adjacent to the lamina perpendicularis of the frontoparietal and within the bony margins of the optic foramen. The trochlear and optic nerves are separated by connective tissue. In more posterior sections, ossification gradually invades the cartilage of the tectum synoticum dorsally, and posterior to the oculomotor foramen, the floor of the neurocranium ventrally. The central part of the tectum, the floor of the neurocranium and the ventrolateral part of the otic capsule are cartilaginous at the anterior level of the acoustic foramen; whereas the dorsal parts of the otic capsule are bony at this level. In the vicinity of the posterior end of the acoustic foramen, the floor of the otic capsule and neurocranium is ossified except for a small ventromedial part of the neurocranial floor which remains cartilaginous. The dorsal part of the otic capsule and the neurocranial roof are almost exclusively cartilaginous at this level. Between the posterior end of the acoustic foramen and the jugular foramen, ossified tissue reappears dorsally; thus, at the level of the jugular foramen, the tectum is restricted to a small dorsomedial area of cartilage and the dorsal parts of the otic capsule are ossified medially but not laterally. The pars externa plectri, pars ascendens plectri, pars interna plectri, operculum, and distal tip of the crista parotica are cartilaginous. The pars media plectri is bony.

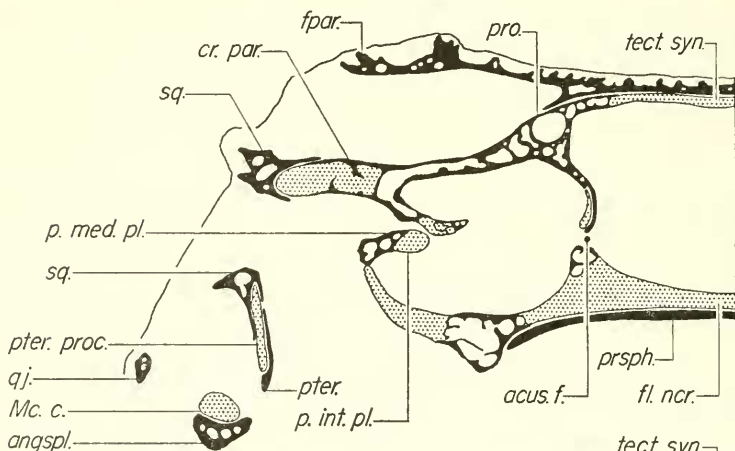
*The Articular Region.*—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenic bone. Posteriorly, the cartilage assumes a position dorsal to the angulosplenic bone and then enlarges and comes to lie in close association with the posterior ramus of the pterygoid, the ventral arm of the squamosal, and the quadrate process. At the posterior level of the acoustic foramen, the posterior ramus of the pterygoid fuses for a short distance with the ventral arm of the squamosal and the ossification of the quadratojugal invades the cartilage of the quadrate process. The pterygoid and squamosal persist posteriorly at the level of the jugular foramen, but the ossification of the quadratojugal has disappeared. Some perichondral ossification appears on the adjacent surfaces of the quadrate process and Meckel's cartilage. The quadrate process is the most posterior element of the articular region.

*Remarks.*—Variation noted among four specimens of *Aparasphenodon bruno*i is ontogenetic and involves the development of dermal bones, principally the prenasal, maxillary, frontoparietal, squamosal, and pterygoid. In a juvenile (head length 13.7 mm.), the external nares lie near the end of the snout, the cristae paroticae are visible in dorsal view, the maxillaries are widely separated anteriorly, the anterior and posterior arms of the squamosal have a poorly developed dorsal flange, and the parasphenoid lacks the transverse ridge characteristic of the adult. In a slightly larger individual (head length 18.6 mm.), the prenasal is better developed anteriorly, but the maxillaries are still widely separated anteroventrally; only the posterolateral corners of the cristae paroticae are visible dorsally because of the lateral growth of the frontoparietal. In this specimen, the parasphenoid bears two prominent lateral knobs; the transverse ridge is not developed. A specimen with a head length of 21.1 mm. has a prominent prenasal. The frontoparietal nearly reaches the squamosal laterally and the dorsal flange of the squamosal is even with the level of the frontoparietal in lateral view. Ventrally, the maxillaries are widely separated anteriorly, but the parasphenoid has developed a weak transverse ridge. The

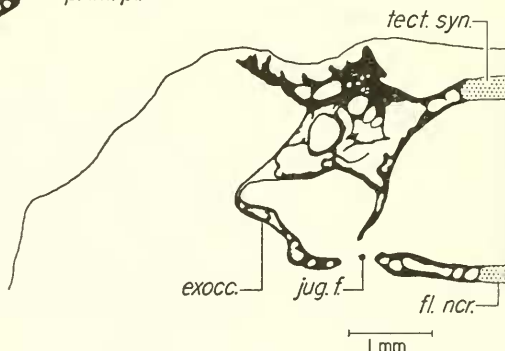
78



79



80



FIGS. 78-80. Transverse sections through the skull of *Aparasphenodon bruni* (KU92214) at levels of cranial nerve foramina: (78) level of prootic foramen; (79) level of acoustic foramen; (80) level of jugular foramen. Abbreviations: *acus. f.*, acoustic foramen; *angspl.*, angulosplenic; *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *jug. f.*, jugular foramen; *max.*, maxillary; *Mc. c.*, Meckel's cartilage; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring.

largest individual (head length 25.4 mm.) is a fully developed adult. In contrast to the smaller specimens, the prenasal extends farther anterior to the external nares making the snout seem highly acuminate by comparison. The extensive posterolateral development of the frontoparietals completely conceals the auditory region in dorsal view. Anteroventrally, the maxillaries are narrowly separated medially thus separating the prenasal anteriorly from the premaxillaries posteriorly. The parasphenoid bears prominent lateral knobs and a well developed transverse ridge.

### Cranial Morphology of *Pternohyla*

The skull of *Pternohyla* is as wide as it is long (*P. dentata*) or slightly wider than long (*P. fodiens*) (Pl. 10a, b). Most of the dorsal surfaces of the skull are involved in integumentary-cranial co-ossification. Dorsally, all dermal bones are covered with small spines which are interconnected by a reticulate network of bony ridges (Pl. 10a). The distal margins of dermal roofing bones, and the squamosals and maxillaries terminate in delicate spinose protuberances. The skull of *Pternohyla* is characterized by a dorsally exposed sphenethmoid, the absence of a dermal sphenethmoid and prenasal, and massive maxillaries which lack extensive labial flanges. The vocal sac is bilobed and subgular. The following description is based on *Pternohyla dentata*, the least specialized member of the genus; differences noted in the cranial morphology of *P. fodiens* will be discussed in a separate section.

*The Olfactory Region.*—The premaxillaries (Fig. 81c, d) are moderately small, and lie slightly recessed to the anterior ends of the maxillaries (Fig. 82). The lateral corners of the premaxillaries are covered by the maxillaries; otherwise, the bones are externally exposed and not involved in integumentary-cranial co-ossification. The premaxillaries are separated medially from one another, and laterally from the maxillaries, by dense connective tissue. Ventromedially, each premaxillary is vertically oriented and about three times as long as the depth of the pars dentalis of the premaxillary. The process is convex anteriorly, and in contact with the alary cartilage and septum nasi dorsally.

In ventral view, the prevomer (Fig. 81d) lies lateral to the mid-line of the skull and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer is associated with the ventrolateral part of the lateral margin of the solum nasi (Fig. 84); the bone lies adjacent to the anteromedial edge of the maxillary. The prevomer does not articulate with the premaxillary. The prevomer bears delicate anterolateral and posterolateral processes which form the anterior and medial margins to the internal nares. The denticerous processes of the prevomer are small and oriented at a slight angle (see Table 1) to the mid-line of the skull. Internally, the prevomer bears a delicate dorsal process which forms a bony support for the olfactory eminence. Posteriorly, the prevomer articulates with the sphenethmoid.

The palatine (Fig. 81d) is a robust bone which lies posterolateral to the internal naris. The distal base of the palatine is broad and flat and lies in connective tissue between the cartilaginous transition zone of the planum antorbitale and solum nasi and the pars palatina of the maxillary. Medially, the palatine articulates with the sphenethmoid posterior to the prevomer. The bone bears a conspicuous longitudinal ridge oriented posteroventrally; the ridge is smooth and the palatine edentate.

The nasal is moderately large (Fig. 81). Anteriorly, the bone terminates in a point at a level just posterior to the alary process of the premaxillary. The nasals converge medially, dorsal to the cartilaginous septum nasi (Fig. 84). At the anterior level of the internal nares the nasals diverge medially to expose dorsally the posterior, ossified part of the septum nasi; the latter is continuous with the sphenethmoid posteriorly. All margins of the nasal are free except the anteromedial edge and the posteroventral corner, which articulates with the

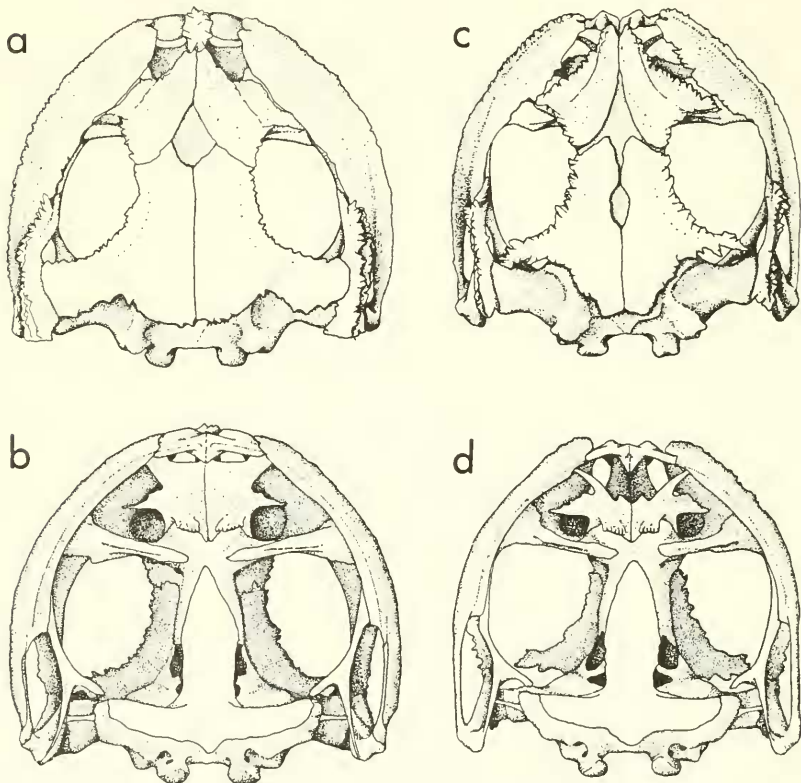


FIG. 81. Skulls of adult *Pternohyla*. (a and b) dorsal and ventral views of the skull of *Pternohyla fodiens*, ♂ (KU 86615); (c and d) dorsal and ventral views of the skull of *Pternohyla dentata*, ♀ (KU 106293).  $\times 3.7$ .

pars facialis of the maxillary. The canthal ridge is only moderately well developed; it extends from the anterior tip of the nasal to the anterodorsal corner of the orbit. The surfaces of the nasal lateral and medial to the canthal ridge are involved in integumentary-cranial co-ossification and are marked by a reticulate network of ridges and small spines. The posterior surface of the maxillary process of the nasal is smooth and is not co-ossified.

The maxillary is massive. The dorsal surface of the maxillary bears integumentary-cranial co-ossification marked by ridge and spines, but the outer edge

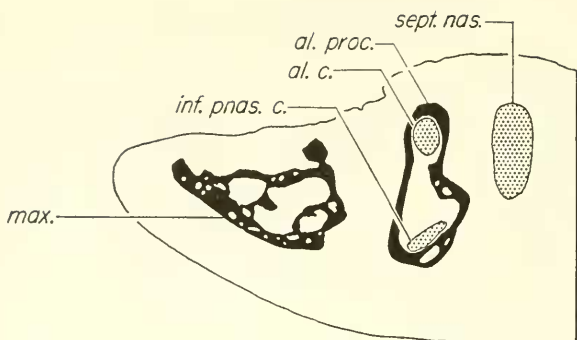
is smooth. Anteriorly (Fig. 84), the pars facialis and pars palatina are well developed. At the anterior margin of the orbit, at the point at which the maxillary articulates with the maxillary process of the nasal, the pars facialis is reduced to a small horizontally oriented shelf which overlies the posterior maxillary process (Fig. 85). Posterior to the pars dentalis and the divergence of the pterygoid and the pterygoid process from the maxillary, the pars palatina and pars facialis terminate (Fig. 86). The maxillary expands dorsally; in cross-section, the long axis of the bone is vertically oriented. The quadratojugal lies medially adjacent to the maxillary (Fig. 87). As the maxillary diminishes in size posteriorly, the quadratojugal increases in size and replaces the former at the level of the anterior acoustic foramen (Fig. 90).

The anterior end of the septum nasi appears between the alary processes of the premaxillaries. Slightly posterior, the superior prenasal cartilage appears on the posterodorsal face of the alary process and the inferior prenasal cartilage on the posteroventral face of the alary process (Fig. 82). The superior prenasal cartilage is closely associated with the alary cartilage posteriorly. The anterior end of the cavum principale is bifid and appears between the tectum nasi and alary cartilage at the anterior level of the overlying nasals. At the level of the anterior margin of the external naris and the cavum medium, the septum nasi expands horizontally and the tectum nasi diverges laterally from the septum nasi as the cartilago obliquus (Fig. 83). The anteromedial recess of the cavum inferius is absent. The anterolateral part of the cavum inferius appears at the level of the foramen of the ramus externus narius and ramus medius narius. In posterior sections, the cavum expands medially. The crista subnasalis is absent. Peripheral ossification appears dorsomedially in the septum nasi at the anterior levels of the olfactory eminence. In more posterior sections, peripheral ossification progresses ventrally and internal ossification centrally. At the anterior level of the internal nares, ossification of the septum nasi is complete, whereas the solum nasi is cartilaginous. The solum nasi is maximally ossified at the posterior margin of the internal nares at the level of the transition zone between the planum antorbitale and anterior maxillary process.

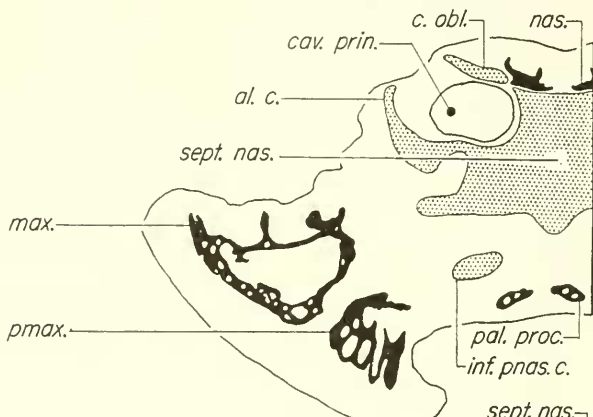
The anterior ramus of the septomaxillary is broad, thin, and slightly concave dorsally. In subsequent posterior sections, the anterior ramus thickens and the anterior end of the ventral spur appears beneath the cavum medium. The anterior ramus diverges into medial and lateral rami. The lateral ramus diminishes in size and persists as a delicate bone which lies adjacent to the margin of the lamina superior. The medial ramus increases in size in a ventromedial direction; it fuses with the dorsally expanding, ventral spur separating the anterior end of the nasolacrimal duct from the cavum medium (Fig. 84). The posterolateral ramus decreases in vertical thickness and in width in a medial direction; the lateral ramus terminates a short distance anterior to the medial ramus.

*The Sphenethmoid and Orbital Region.*—The frontoparietals converge medially throughout their lengths in some specimens; in other individuals (Fig. 81), they diverge in the orbital region to produce a small frontoparietal fontanelle anterior to the level of the optic foramen. All distal margins of the frontoparietal are free. The lateral edge extends over the orbit to form a narrow supraorbital flange and expands posterolaterally into a prominent lateral process which lies over the posterior part of the orbit anterodorsal to the prootic. The

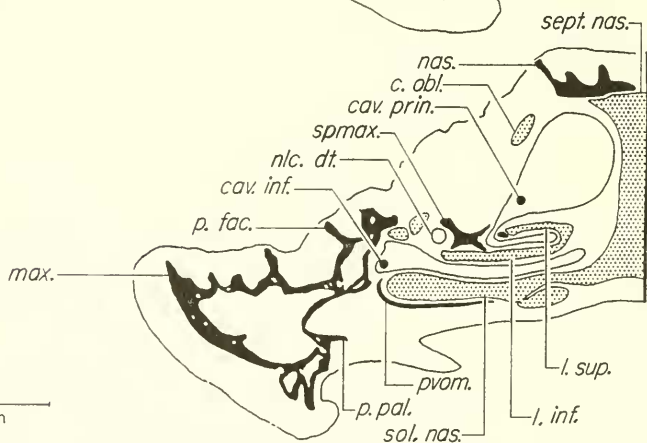
82



83



84



FIGS. 82-84. Transverse sections through anterior end of skull of *Pterohyla dentata* (KU 111989): (82) level of alary process of premaxillary; (83) anterior level of cavum principale; (84) posterior level of septomaxillary. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *c. obl.*, cartilago obliquus; *cav. inf.*, cavum inferius; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *p. fac.*, pars facialis of maxillary; *p. pal.*, pars palatina of maxillary; *pal. proc.*, palatine process of premaxillary; *pmax.*, premaxillary; *pvom.*, prevomer; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary.

dorsal surface of the frontoparietal is covered with a fine, reticulate network of ridges and spines. The lateral supraorbital margin of the frontoparietal terminates in a small, upturned flange of spines.

The dermal sphenethmoid is absent in *Pternohyla*. The dermal roofing bones do not converge medially and part of the sphenethmoid is visible (Pl. 10a; Fig. 81a, c). The dorsal surface of the sphenethmoid is smooth and is not involved in integumentary-cranial co-ossification (Fig. 85). The sphenethmoid is in synosteotic continuity with the septum nasi anteriorly. Internally, the sphenethmoid is separated from the overlying nasals and frontoparietals by a thin layer of dense connective tissue. The sphenethmoid is bony anterior to the orbitonasal foramen; at the level of the foramen (Fig. 85), a small amount of cartilage is located at the distal tip of the anterolateral wing of the sphenethmoid underlying the nasal. This cartilage persists for a short distance posterior to the orbitonasal foramen, and then disappears. Ventral to the frontoparietals in the mid-orbit region, the roof of the sphenethmoid splits to form the frontoparietal fontanelle (Fig. 86); the fontanelle extends posteriorly to the anterior level of the optic foramen. Dense connective tissue, which separates the sphenethmoid and frontoparietal, is continuous across the frontoparietal fontanelle ventral to the frontoparietals in all specimens. In some individuals, the frontoparietals diverge to expose the fontanelle dorsally. The sphenethmoid is completely bony at the anterior level of the frontoparietal fontanelle; a short distance posterior, the taenia tecti marginalis appear. At the anterior level of the optic foramen, the sphenethmoid is completely cartilaginous. The posterior border of the frontoparietal fontanelle is formed in cartilage by the tectum synoticum.

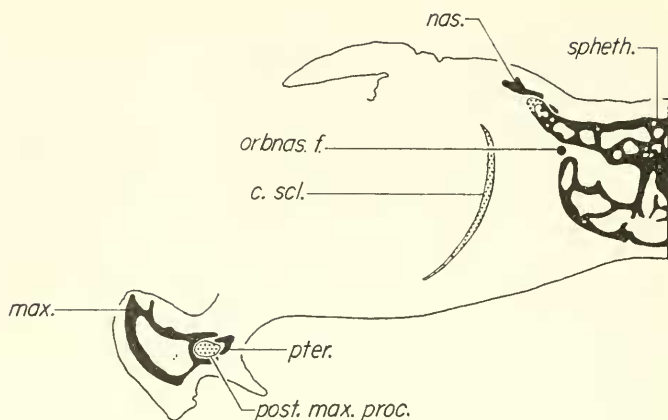
An isolated rod of cartilage lies ventromedial to the sphenethmoid at the level of the articulation of the palatines with the sphenethmoid. The cartilage is round in cross-section and about 0.32 mm. long. It lies in the dense connective tissue connecting the medial tips of the palatines across the venter of the sphenethmoid, but is otherwise unassociated with cranial elements.

The anterior end of the parasphenoid lies just posterior to the level of the orbitonasal foramen. The bone lies ventral to the sphenethmoid and prootic, and forms a bony bridge of support for the neurocranial floor at the synchondrotic union of the sphenethmoid and prootic. The parasphenoid is separated from adjacent bones by connective tissue. The bone is smooth and edentate.

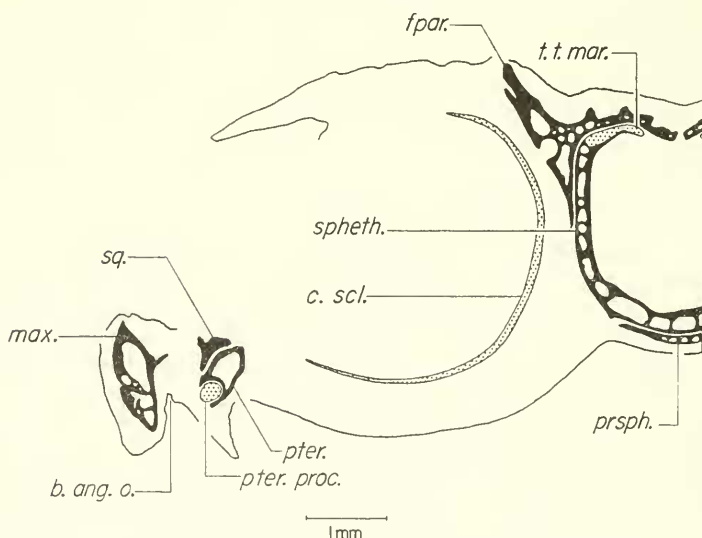
The bursa angularis oris (Fig. 86) is small and lies in the mid-orbital region at the anterior levels of the frontoparietal foramen. The bursa lies between the maxillary and the pterygoid process. It has no distinct central lumen as do the glands of *Tripriion spatulatus* and *Smilisca baudini*; the structure of the gland resembles that of *Tripriion petasatus* in being an unorganized mass of lymphoid tissue.

*The Otic and Occipital Regions.*—In dorsal view (Fig. 81c), the squamosal is a long, slim bone which extends from the mid-orbital region posterior to the posterior margin of the prootic. The dorsal and dorsolateral surfaces of the head of the squamosal are completely involved in integumentary-cranial co-ossification. The anterior arm of the squamosal is moderately robust and forms the bony posterior margin of the orbit; it terminates ventrally, on the dorsal surfaces of the pterygoid and maxillary at the level just posterior to the articulation of the maxillary and pterygoid (Fig. 86). A thin layer of dense

85



86



FIGS. 85-86. Transverse sections through mid-region of skull of *Pternohyla dentata* (KU 111989): (85) level of orbitonasal foramen; (86) posterior region of orbit. Abbreviations: *b. ang. o.*, bursa anularis oris; *c. scl.*, cartilaginous sclera; *fpar.*, frontoparietal; *max.*, maxillary; *nas.*, nasal; *orbnas. f.*, orbitonasal foramen; *post. max. proc.*, posterior maxillary process; *prsph.*, parasphegoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *spheth.*, sphenethmoid; *sq.*, squamosal; *t. t. mar.*, taenia tecta marginalis.

connective tissue separates the anterior arm of the squamosal and the anterior ramus of the pterygoid. The posterior arm of the squamosal is equally as robust as the anterior arm, but unlike the latter, the posterior arm is straight and does not extend ventrally toward the maxillary. The ventral arm of the squamosal extends posteroventrally from the mid-point of the arc formed by the anterior and posterior arms of the squamosal; posteroventrally, the terminus lies between the quadratojugal and the posterior ramus of the pterygoid (Fig. 91).

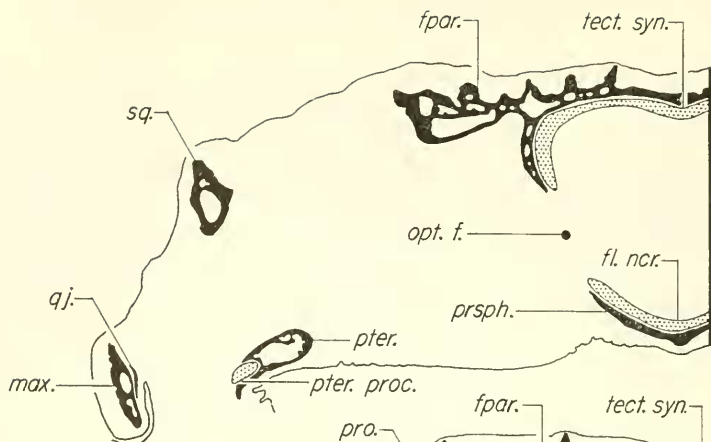
The pterygoid is moderately large (Fig. 81d). The anterior end of the anterior ramus lies in connective tissue adjacent to the posterior maxillary process and pars facialis of the maxillary at a level posterior to the palatines and anterior to the orbitonasal foramen (Fig. 85). In posterior sections, the anterior ramus increases in size and encases the medial surface of the posterior maxillary process. At the posterior terminus of the pars dentalis in the mid-orbital region, the anterior ramus of the pterygoid and the pterygoid process diverge medially from the maxillary (Fig. 86). The medial ramus is reduced and does not articulate with the prootic; it terminates at a level just anterior to the oculomotor foramen (Fig. 88). The posterior ramus articulates dorsally with the ventral arm of the squamosal, and posteriorly, lies medially adjacent to the quadrate process.

In cross-section, the quadratojugal is a long, narrow bone vertically oriented. It appears medial to the maxillary at the level of the optic foramen (Fig. 87). In successively posterior sections, the quadratojugal increases in size and the maxillary decreases in size; at a level just posterior to the prootic foramen, the maxillary terminates. Posteriorly, the quadratojugal decreases in size. At the posterior end of the quadratojugal, it lies ventrolateral to the ventral arm of the squamosal and is involved in ossification of the quadrate process.

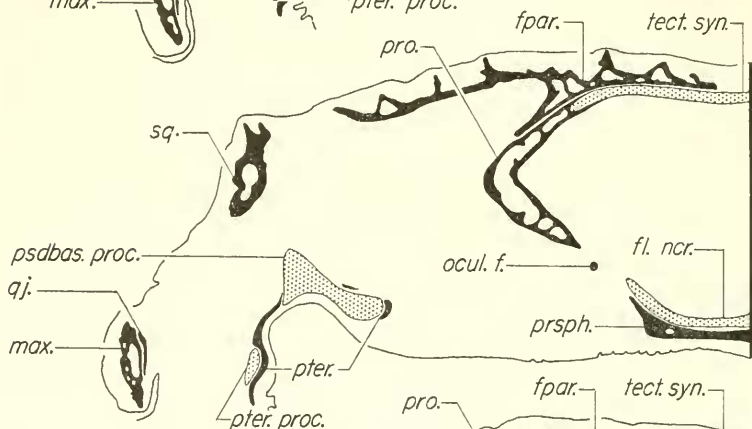
The anterior part of the optic foramen lies in the posterior, cartilaginous part of the sphenethmoid. The posterior and dorsal margins of the foramen are bony and formed by the prootic and lamina perpendicularis of the frontoparietal (Fig. 87). The trochlear foramen lies dorsal to the optic foramen in the lamina perpendicularis of the frontoparietal. The oculomotor foramen (Fig. 88) lies posteroventral to the optic foramen; dorsally, the foramen is bordered by bone and ventrally and posteriorly by cartilage. An extremely narrow bridge of bone separates the oculomotor foramen from the prootic foramen (Fig. 89); the latter lies immediately posterior and dorsal to the oculomotor foramen. The prootic foramen is bordered entirely by bone. The anterior acoustic foramen (Fig. 90) lies at the mid-level of the operculum posterior to the pars interna plectri and is bordered by bone. A bridge of bone and cartilage separates the anterior acoustic foramen from the posterior acoustic foramen (Fig. 91) at the posterior levels of the operculum. The posterior acoustic foramen is bordered by bone and lies just anterior to the level of the jugular foramen (Fig. 92).

The pseudobasal and otic processes appear just posterior to the optic foramen. The pseudobasal process (Fig. 88) lies lateral to the neurocranium; in posterior sections, the pseudobasal process expands dorsally into the otic process which lies medial to the dorsal part of the anterior arm of the squamosal. Posteriorly, the ventral part of this block of cartilage bifurcates vertically (in cross-section) to produce medial and lateral branches. The medial branch is continuous with the pseudobasal process. The lateral branch first diverges posteroventrally from the otic process and then fuses ventrally with the pterygoid process. At the level of the divergence of the dorsal and ventrolateral parts of the otic process, the medial branch splits, separating the otic process dorsally from the pseudobasal process ventrally. In subsequent sections, the otic process ossifies proximally and becomes horizontally oriented as the crista parotica (Fig. 89). The crista parotica joins the medial part of the otic capsule and the lateral part of the pseudobasal process diverges as the cornu principalis of the hyale at the posterior level of the oculomotor foramen.

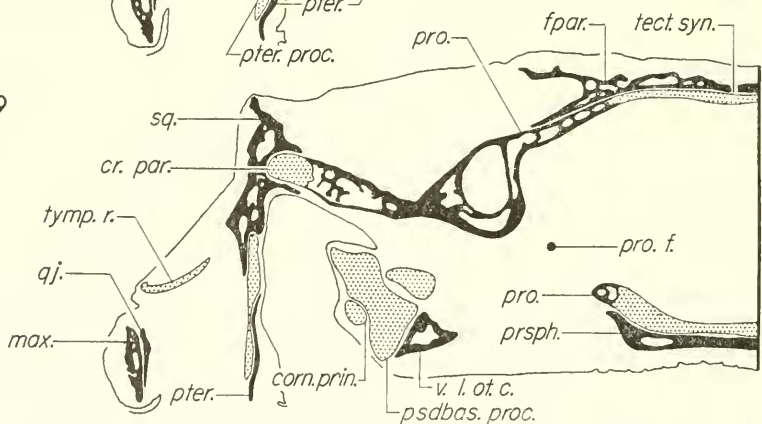
87



88



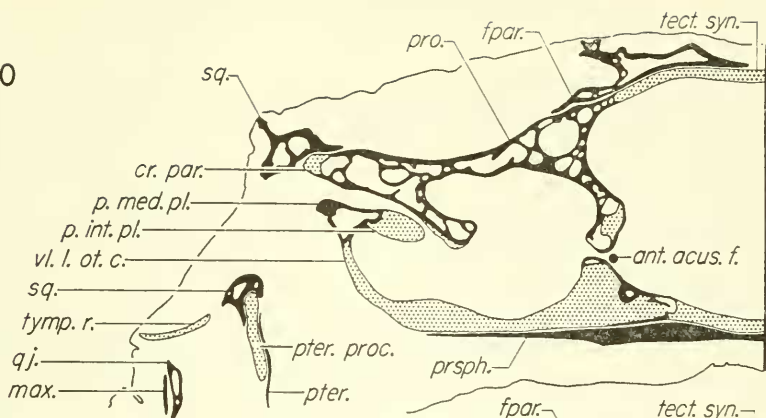
89



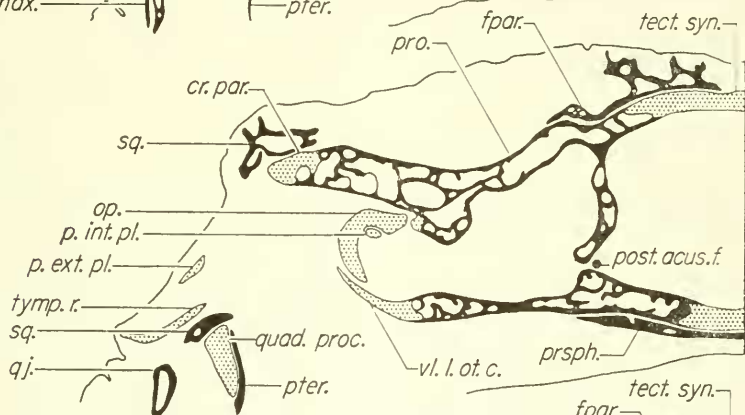
1 mm

FIGS. 87-89. Transverse sections through skull of *Pternohylla dentata* (KU 111989) at levels of cranial nerve foramina: (87) level of optic foramen; (88) level of oculomotor foramen; (89) level of prootic foramen. Abbreviations: *corn. prin.*, cornu principalis; *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadrate jugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring; *v. l. ot. c.*, ventral ledge otic capsule.

90



91



92

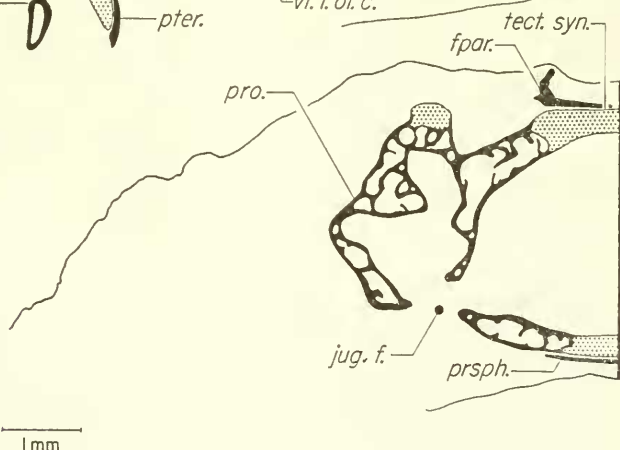


FIG. 90-92. Transverse sections through skull of *Pteronohyla dentata* (KU 111989) at levels of cranial nerve foramina: (90) level of anterior acoustic foramen; (91) level of posterior acoustic foramen; (92) level of jugular foramen. Abbreviations: *ant. acus. f.*, anterior acoustic foramen; *cr. par.*, crista parotica; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *jug. f.*, jugular foramen; *max.*, maxillary; *op.*, operculum; *p. ext. pl.*, pars externa plectri; *p. int. pl.*, pars interna plectri; *p. med. pl.*, pars media plectri; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *qj.*, quadratojugal; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring; *v. l. ot. c.*, ventrolateral ledge of otic capsule.

The ventrolateral ledge of the otic capsule appears anteriorly at the anterior level of the prootic foramen. The pars interna plectri and pars externa plectri appear at the posterior level of the prootic foramen. In sections just posterior to the appearance of the latter structures, the pars ascendens plectri appears in association with the distal tip of the crista parotica. Posterior to the pars ascendens plectri and the prootic foramen, the pars media plectri appears. The anterior end of the operculum lies anterior to the level of the posterior acoustic foramen. The operculum terminates at the posterior level of the posterior acoustic foramen.

At the posterior level of the optic foramen, the prootic is ossified only ventrolaterally dorsal to the foramen; the floor of the neurocranium is cartilaginous. In posterior sections, ossification increases ventromedially in the neurocranium. At the level of the oculomotor foramen, the sides of the braincase are bony; whereas the roof and floor of the neurocranium are cartilaginous. Some ossification invades the floor of the otic capsule at the level of the anterior acoustic foramen, but the ventrolateral ledge of the otic capsule, the distal tip of the crista parotica, and the roof and dorsomedial part of the floor of the neurocranium remain cartilaginous. The pars media plectri is bony. The pars externa plectri, pars ascendens plectri, pars interna plectri, and operculum are cartilaginous. Posterior to the operculum, at the level of the jugular foramen, the otic capsule is bony except for a small dorsal tip; at this level and posterior, the dorsomedial and ventromedial parts of the neurocranium are cartilaginous.

*The Articular Region.*—Anterior to the articular region, Meckel's cartilage lies dorsal and slightly lateral to the angulosplenial bone. Posteriorly, the cartilage enlarges, moves dorsally, and comes to lie in close association with the ventral arm of the squamosal, the quadratojugal, posterior ramus of the pterygoid, and the quadrate process. At a level slightly anterior to the anterior acoustic foramen, the quadratojugal invades the cartilage of the quadrate process. The quadratojugal, squamosal, and pterygoid remain separated throughout their respective lengths. At the posterior level of the operculum and the posterior acoustic foramen, the quadrate process is cartilaginous and is bordered dorsolaterally by the posteroventral terminus of the squamosal and dorsomedially by the posterior ramus of the pterygoid. Both the squamosal and pterygoid terminate at the posterior margin of the posterior acoustic foramen.

*Pternohyla fodiens.*—The most obvious differences between the skulls of *Pternohyla fodiens* and *P. dentata* involve the dermal bones. The relative dimensions of the dermal roofing bones are greater in *P. fodiens* (Fig. 81a) and the maxillary has a shallow, but well developed labial flange. The presence of the labial flange accounts for the greater width of the skull as compared with *P. dentata*. The medial ramus of the pterygoid articulates with the prootic. Internally, the cranial structures of the two species are similar, although the skull of *P. fodiens* is more extensively ossified and some minor structural differences occur in the otic region. In the following discussion, only differences in the cranial structure of *P. fodiens* as compared with *P. dentata* are described. The description of *P. dentata* applies to all structures and regions which are not specifically mentioned below.

The most striking external difference in the olfactory region of *Pternohyla fodiens* is the presence of an anteromedial dermal bone, here termed the in-

ternasal (*intnas.*), because of its position medial to the external nares and the anterior tips of the nasals (Pl. 10a; Fig. 81a). The anterior end of the internasal lies anterior to the premaxillary. The dorsal surface is involved in integumentary-cranial co-ossification and bears bony ridges. In cross-section, the internasal is a wedge-shaped bone which extends posteriorly between the alary processes of the premaxillaries (Fig. 93). At the level of the pars dentalis of the premaxillary, the internasal lies dorsomedial to the alary processes of the premaxillary. Posteriorly, just anterior to the external nares (Fig. 94), the internasal lies dorsomedial to the septum nasi and is flanked ventrolaterally by well developed tecta nasi which support the medial margins of the nostrils. The internasal diminishes in size posteriorly, and near the posterior margin of the external nares is underlain by the anterior ends of the pared nasals (Fig. 95). A short distance posterior to the external nares, the internasal terminates.

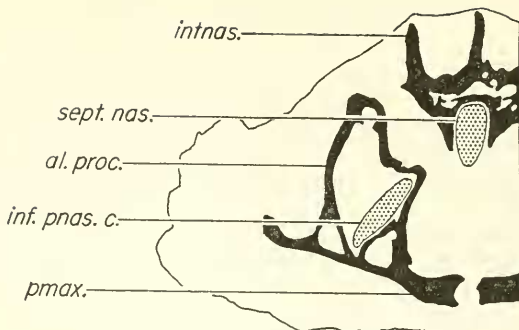
The premaxillary is much more robust in *Pternohyla fodiens* than in *P. dentata*. The alary process of the premaxillary is wide and thick; because of this, the anterior end of the premaxillary is even with the anterior ends of the maxillaries, rather than being recessed. The anterior surfaces of the alary processes are pitted and rugose and involved in integumentary-cranial co-ossification. Ventrally (Pl. 10b; Fig. 81b), the prevomer is much larger than in *P. dentata*. The anterolateral corner lies adjacent to the solum nasi, dorsal to the posterolateral corner of the pars dentalis of the premaxillary. In larger individuals, the prevomers converge medially, posterior to the palatine processes of the premaxillary. The nasal of *P. fodiens* is larger than that of *P. dentata*. The medial convergence of the nasals is greater and the anterolateral part of the bone is more extensive. The posterodorsal margin of the nasal articulates with the anterior margin of the frontoparietal. The canthal ridge is well developed and extends from the anteromedial tip of the nasal to the anterodorsal corner of the orbit.

The anterior end of the septum nasi appears between the alary processes of the premaxillaries ventral to the internasal (Fig. 93). The disposition of the inferior and superior prenasal cartilage is as described for *Pternohyla dentata*; *P. fodiens* also lack a crista subnasalis. The anterior end of the cavum principale is double and appears within the alary cartilage instead of lateral to it. The cavum medium appears just posterior to the anterior end of the cavum principale anterior to the level of the external nares. The anteromedial recess of the cavum inferius and the crista subnasalis are absent.

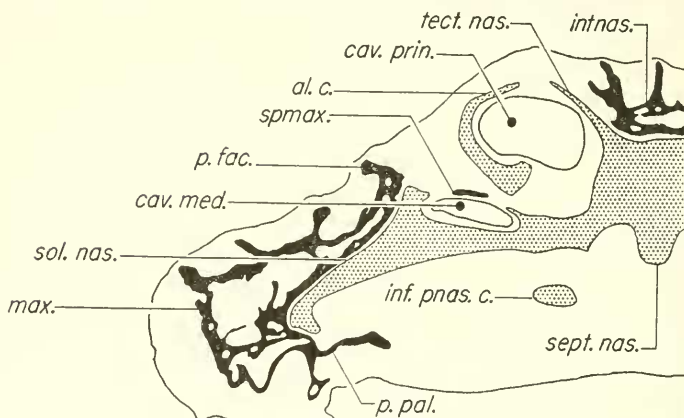
The frontoparietal articulates anteriorly with the nasal and posterolaterally with the squamosal. Anterolaterally, the frontoparietal extends over the orbit as a bony shelf. The frontoparietals converge medially throughout most of their lengths. The posterior margin of the frontoparietal terminates dorsal to the exoccipital and crista parotica. The frontoparietals and nasals do not converge medially in *Pternohyla fodiens*; thus a small part of the sphenethmoid is visible. Because the frontoparietals and nasals are larger in *P. fodiens*, less of the sphenethmoid is exposed dorsally than in *P. dentata*. Internally, ossification of the sphenethmoid is more extensive posteriorly in *P. fodiens* than in *P. dentata*. There is no isolated rod of cartilage ventromedial to the sphenethmoid.

The pseudobasal process does not appear until the anterior level of the prootic foramen. Slightly posterior, the anterior end of the otic process lies medially adjacent to the anterior arm of the squamosal. In posterior sections

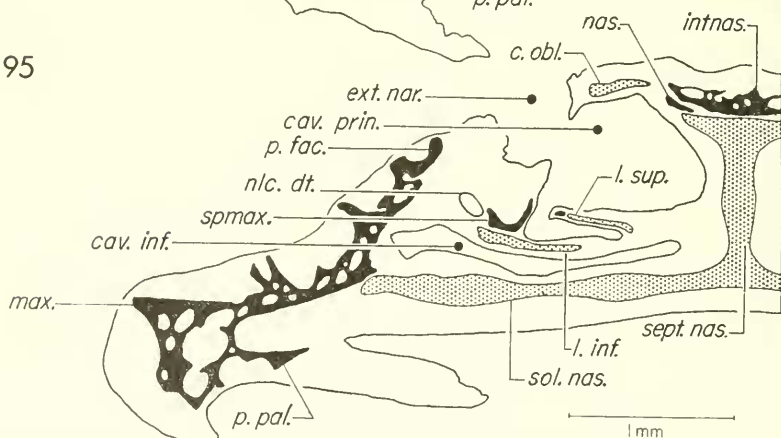
93



94



95



FIGS. 93-95. Transverse sections through anterior end of skull of *Pterohyla fodiens* (KU 89925) in region of internasal: (93) level of alary process of premaxillary; (94) anterior levels of cavum medium and cavum principale; (95) posterior level of septomaxillary. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *c. obl.*, cartilago obliquus; *cav. inf.*, cavum inferius; *cav. med.*, cavum medium; *cav. prin.*, cavum principale; *ext. nar.*, external nares; *intrnas.*, internasal; *inf. pnas. c.*, inferior prenasal cartilage; *l. inf.*, lamina inferior; *l. sup.*, lamina superior; *max.*, maxillary; *nas.*, nasal; *nlc. dt.*, nasolacrimal duct; *p. fac.*, pars facialis of maxillary; *p. pal.*, pars palatina of maxillary; *pmax.*, premaxillary; *sept. nas.*, septum nasi; *sol. nas.*, solum nasi; *spmax.*, septomaxillary.

at the mid-level of the prootic foramen, the otic process expands medially to meet the otic capsule as the crista parotica; in subsequent sections, the pseudobasal and pterygoid processes diverge ventrally from the crista parotica. The ventrolateral ledge of the otic capsule appears posterior to the prootic foramen. The pars media plectri appears at the anterior level of the acoustic foramen. The appearance of the pars interna plectri in subsequent sections is followed by the pars externa plectri, pars ascendens plectri, and operculum, respectively. There is only one acoustic foramen.

*Remarks.*—Smith (1957) stated in his diagnosis of *Pternohyla dentata* that the species possesses parasphenoid “teeth.” None of the specimens that I have examined possess any type of parasphenoid odontoids. In his comparisons of *P. dentata* and *P. fodiens*, he pointed out that the palatine is ridge-like and with tooth-like irregularities in *P. dentata*, whereas the palatine is less elevated and lacks denticulations in *P. fodiens*. I agree that the palatine ridge is smoother in *P. fodiens*; however, I find no differences in the degrees of development of the ridges and hesitate to refer to the small irregularities of *P. fodiens* as “denticulations.”

The only variation noted among specimens of *Pternohyla* involves ossification of dermal roofing bones. In all individuals, the sphenethmoid is exposed dorsally. The size of the exposed part of the sphenethmoid, the presence of a dorsally exposed frontoparietal fontanelle, and the extensiveness of frontoparietal flanges depends on the development of the dermal roofing bones. Small specimens tend to have less well developed nasals and frontoparietals. Integumentary-cranial co-ossification is more extensive in larger specimens. Co-ossification is never complete; the nasal at the anterior margin of the orbit, the sphenethmoid, and the exposed, dorsal surface of the prootic are not co-ossified. In small individuals, the skin dorsal to the medial convergence of the frontoparietals is not co-ossified.

The basic structure of the skull of *Pternohyla* bears a striking resemblance to the cranial morphology of *Smilisca baudini* (see Duellman and Trueb, 1966, and Trueb, 1968). The shape of the skull and the relative sizes and shapes of the individual bones are similar. Comparison of the dorsal aspects of the skull of *S. baudini* and *P. dentata* (Fig. 96) shows that the latter can be derived from the former by the following changes: increase the size of the nasal to overlap the septum nasi and sphenethmoid dorsally, and extend the nasal toward the maxillary ventrolaterally; increase the size of the frontoparietal to overlap the sphenethmoid, and extend the supraorbital flanges of the frontoparietal posterolaterally over the rear of the orbit; increase the size of the maxillary, extending the pars facialis and creating a shallow labial flange along the outer margin of the maxillary; and increase the size of the squamosal. Ventrally, one need only extend the anterolateral wing of the prevomer, extend the anterior ramus of the pterygoid anteriorly, and eliminate the connection between the posterior ramus of the pterygoid and the prootic. Internally, only minor differences exist between the skulls of *Pternohyla* and *S. baudini*. Less cartilage exists in *P. dentata* than in *S. baudini*. *S. baudini* has a crista subnasalis and a medial recess of the cavum inferius; *Pternohyla* lacks these structures. The otic region is more extensive in an anterior-posterior direction in *P. dentata* than in *S. baudini*; however, the structure of the otic region in *P. fodiens* very closely resembles that of *S. baudini*. *P. fodiens* differs from the latter in having

one large acoustic foramen rather than two acoustic foramina. *Pterohyla fodiens* can be derived from *S. baudini* in the same manner as *P. dentata* by expansion of the dermal roofing bones and addition of the internasal bone anteriorly.

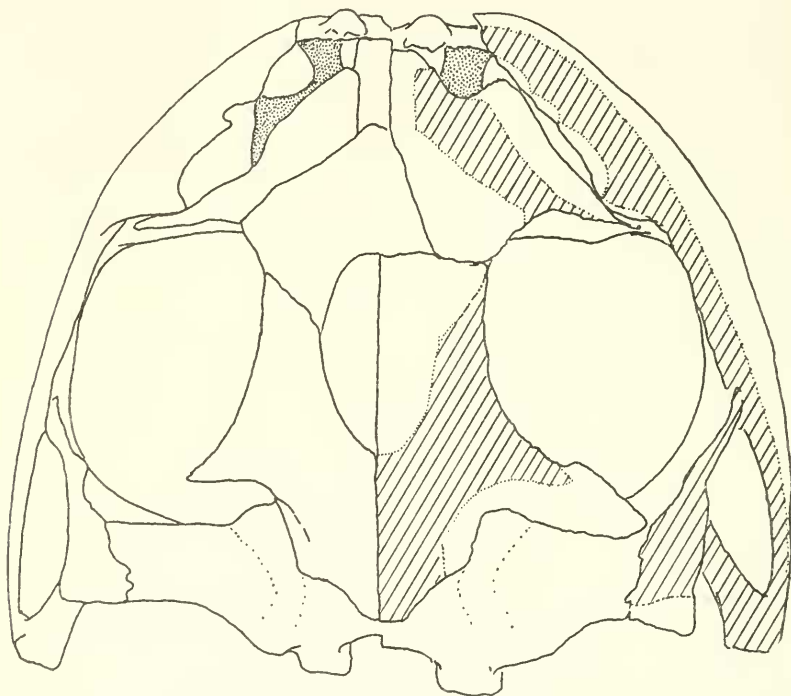


FIG. 96. Composite view of the skulls of *Pterohyla dentata* (KU 106293) and *Smilisca baudini* (KU 68184) approximately  $\times 3$ . Left half drawing represents *Smilisca baudini* and right half *Pterohyla dentata*. Structure of *S. baudini* is superimposed in cross-hatching on right side of figure.

### Cranial Morphology of *Triprrion spatulatus*

The skull of *Triprrion spatulatus* is considerably longer than it is wide (Pl. 11a, b). All dorsal surfaces of the skull except the sphenethmoid are involved in integumentary-cranial co-ossification. Dorsally, all dermal bones are finely sculptured in a pattern of parallel or reticulate ridges. The distal margins of all dermal bones terminate in spinose protuberances; the latter are best developed on the outer edges of the maxillary and prenasal, the canthal ridge near the orbit, and the occipital crest. The skull of *Triprrion spatulatus* is characterized by having no part, or only a small part, of the sphenethmoid exposed dorsally, by the absence of a dermal sphenethmoid, the presence of a prenasal, and an extensive labial flange on the maxillary and prenasal anterior to the orbit. The vocal sac is single, median, and subgular.

*The Olfactory Region.*—The prenasal (Pl. 11a, b) lies anterior to the premaxillaries and nasals and between the anterior ends of the maxillaries. The

bone is flat ventrally; dorsally, it bears a prominent medial ridge and a flat, spinose labial flange. The dorsal surface of the bone is sculptured in longitudinal ridges medially and a reticulate pattern of ridges laterally. Posterolaterally, the prenasal articulates with the maxillary; posteromedially, it overlaps the anterior margin of the external nares. Ventromedially, the prenasal lies adjacent to the premaxillaries. Internally, the anterior part of the prenasal contains many small cavities (Fig. 97). A short distance posteriorly, the cavities coalesce to form a single, large, central cavity that is vertically oriented (Fig. 98). At about one-half the length of the prenasal, the vertical cavity is depressed ventrally and oriented horizontally; subsequently, it is divided into many smaller cavities. Two large, dorsal cavities, housing the anterior ends of the nasal capsules and alary processes of the premaxillaries, appear just anterior to the opening of the external nares (Fig. 99). There is an incomplete prenasal septum, which lies ventral to the septum nasi and separates the alary processes of the premaxillary throughout their lengths. The prenasals of the two subspecies of *Triprrion spatulatus* differ slightly in shape. The prenasal of *T. s. spatulatus* has a broad medial ridge and is triangular in cross-section, whereas that of *T. s. reticulatus* has a narrower medial ridge and is shaped like an inverted "T" in cross-section.

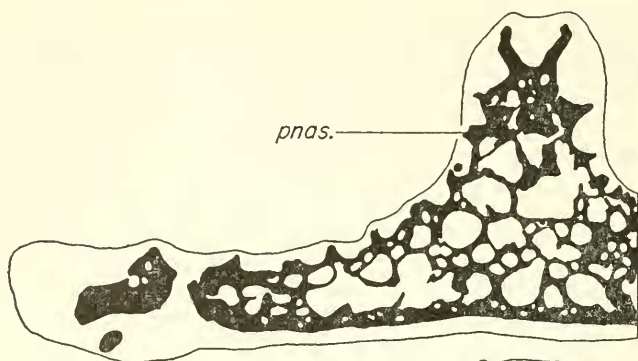
The premaxillaries are narrowly separated medially by connective tissue. Laterally, the premaxillary is separated from the pars palatina and the pars dentalis of the maxillary by an area of dense connective tissue. A small, inconspicuous palatine process is present posteromedially on the premaxillary. The alary processes of the premaxillary are inclined anteriorly at a 45-degree angle. The processes are straight and approximately five times as long as the depth of the pars dentalis of the premaxillary. The anterior two-thirds of the alary processes lie inside of the prenasal.

In ventral view (Pl. 11b), the prevomer lies lateral to the midline of the skull and ventral to the solum nasi and sphenethmoid. The anterior end of the prevomer lies dorsal to the articulation between the pars palatina of the maxillary and premaxillary. The posterior dentigerous part of the bone lies at a slight angle or perpendicular to the midline. The prevomer bears well developed, lateral wings that form the anterior, medial, and posteromedial margins of the internal naris. Internally, the prevomer bears a dorsal extension which supports the olfactory eminence.

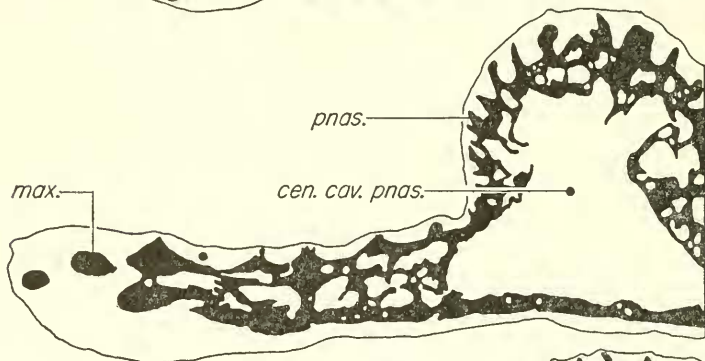
The palatine is a narrow, thin bone which lies posterolateral to the internal naris. The broad, distal end is lodged in connective tissue dorsal to the pars palatina of the maxillary and adjacent to the anterior maxillary process. The delicate, proximal end lies ventral to the lateral edge of the sphenethmoid and is separated from the sphenethmoid by a thin layer of loose connective tissue. The palatine bears a series of odontoids along the prominent ventral ridge.

The nasal is extremely large (Pl. 11a). Anteriorly, the nasal articulates with the prenasal, except where the former forms the posterior margins of the external nares. Laterally, the nasal articulates with the pars facialis of the maxillary, and posterolaterally, it forms the bony anterior margin of the orbit. The nasals converge anteromedially to the dorsally exposed part of the sphenethmoid. The posterior margin of the nasal articulates with the anterodorsal margin of the frontoparietal; a thin ventral flange of the frontoparietal underlies the posterior margin of the nasal. The dorsal surface of the nasal is completely involved in integumentary-cranial co-ossification. The nasal bears a well developed canthal ridge extending from the posteromedial margin of the external

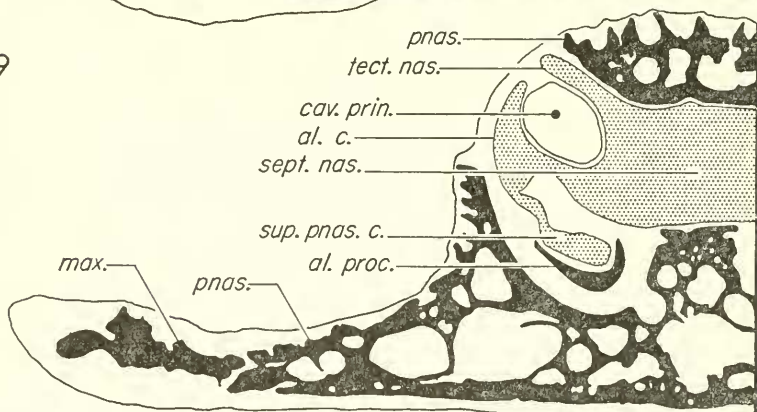
97



98



99



1 mm

FIGS. 97-99. Transverse sections through prenasal and anterior end of olfactory capsule of *Tripurion spatulatus* (KU 86925): (97) anterior end of prenasal; (98) prenasal at level of central cavity; (99) anterior level of cavum principale. Abbreviations: *al. c.*, alary cartilage; *al. proc.*, alary process of premaxillary; *cav. prin.*, cavum principale; *cen. cav. pnas.*, central cavity of prenasal; *max.*, maxillary; *pnas.*, prenasal; *sept. nas.*, septum nasi; *sup. pnas. c.*, superior prenasal cartilage; *tect. nas.*, tectum nasi.

naris to the anterodorsal corner of the orbit, where a proliferation of small spines is present on the ridge. Lateral and medial to the canthal ridge, the surface of the nasal is marked by a fine reticulate network of ridges. The supraorbital margin of the nasal bears a series of small spines.

The maxillary is moderately robust. Anterior to the orbit, the maxillary bears a broad flange, which is deeply concave dorsally in front of the orbit and nearly flat anteriorly at its articulation with the prenasal. An inconspicuous flange, consisting of a row of small spines, is present along the lateral edge of the maxillary, ventral and posterior to the orbit. The dorsal and lateral surfaces of the maxillary are involved in integumentary-cranial co-ossification. The labial flange is sculptured into a series of fine ridges that terminate in long spines distally. The pars facialis of the maxillary is marked by a fine reticulate network of ridges. Medially, the maxillary bears a pars palatina (Fig. 100) extending the length of the bone dorsal to the pars dentalis. The pars palatina is best developed anterior to the orbit; posterior to the orbit, the pars palatina is barely evident. Dorsal to the pars palatina and anterior to the orbit, the maxillary bears a large pars facialis; the latter lies adjacent to the nasal anteriorly, and posteriorly forms the bony ventral margin to the orbit. Slightly posterior to the terminus of the pars dentalis, the quadratojugal lies ventromedial to the maxillary. A thin area of dense connective tissue separates the quadratojugal and maxillary.

The anterior end of the nasal capsule lies forward within the prenasal (Fig. 99). The cartilaginous septum nasi projects anteriorly into a medial cavity of the prenasal. This cavity is flanked laterally by two other cavities, each of which contains the anterior end of the alary process of the premaxillary and the associate superior prenasal cartilages. At the level of the anterior margin of the external nares the septum nasi expands horizontally, thereby separating the prenasal into a dorsal and ventral component. The anterior end of the cavum principale is bifurcate, and is encased by the alary cartilage, tectum nasi, and septum nasi, and lies at the same level. The tectum nasi is exceptionally short, extending only from the anterior end of the cavum principale to the anterior end of the cavum medium in *Triprioron spatulatus reticulatus*. In *T. s. spatulatus*, the tectum terminates anterior to the appearance of the cavum medium. The superior and inferior prenasal cartilages are well developed. The former lies anteroventral to the alary cartilage, extending from the cartilage to the posterior surface of the alary process of the premaxillary. The inferior prenasal cartilage appears on the posteromedial face of the alary process of the premaxillary, extends dorsally and fuses with the solum nasi at the posterior levels of the septomaxillary in *T. spatulatus reticulatus* and posterior to the septomaxillary in *T. s. spatulatus*. Both species have a crista subnasalis and anterior maxillary process. The nature of the nasal cavities and associated cartilages is the same as that described for *Triprioron petasatus*. Peripheral ossification of the septum nasi appears at the anterior levels of the olfactory eminence. Ossification spreads from central to peripheral parts of the septum in successively more posterior sections, and at the anterior level of the internal nares, both the septum and solum nasi are entirely ossified. Posteriorly, the septum nasi is continuous with the sphenethmoid. The septomaxillary of *T. spatulatus* resembles that of *T. petasatus*. The septomaxillary lacks the distinct dorsal ramus characteristic of the bone in *T. petasatus*; the lateral ramus is more robust, and medial branch is weaker by comparison.

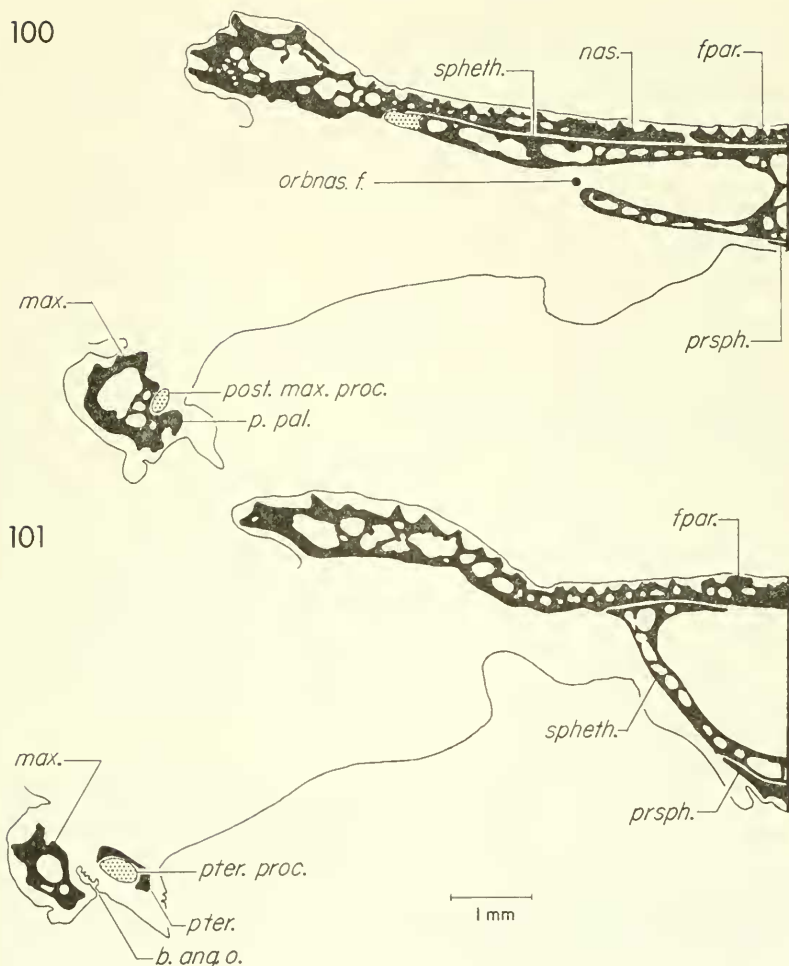
*The Sphenethmoid and Orbital Region.*—The frontoparietal (Pl. 11a) is a rectangular element which articulates anteriorly with the posterior margin of the nasal and posterolaterally with the squamosal. Anterolaterally, the frontoparietal extends over the orbit as a bony shelf. The frontoparietals articulate medially throughout their entire lengths. The posterior margin of the frontoparietal terminates in an upturned, spinose occipital crest. Ventral to the occipital crest, the frontoparietal is attached to the exoccipital; laterally, it bridges the prootic from the exoccipital to the squamosal. The dorsal surface of the frontoparietal is involved in integumentary–cranial co-ossification. The supraorbital part of the frontoparietal is marked by a pattern of parallel ridges which run from the center of the bone to the margin of the orbit where they terminate in small spines. The rest of the surface of the frontoparietal bears a reticulate network of ridges.

The dermal sphenethmoid is absent in *Tripriion spatulatus*. In most males and all but the large females the nasals do not meet one another posteromedially (Pl. 11a) and a small part of the sphenethmoid is visible. The dorsal surface of the sphenethmoid is smooth and is not involved in integumentary–cranial co-ossification. The sphenethmoid is in synchondrotic continuity with the septum nasi anteriorly. Internally, the sphenethmoid is separated from the overlying nasals and frontoparietals by a thin layer of dense connective tissue. At the level of, and anterior to, the orbitonasal foramen (Fig. 100), a small amount of cartilage is located at the distal tip of the anterolateral wing of the sphenethmoid underlying the nasal. The rest of the sphenethmoid is bony posterior to the anterior margin of the optic foramen; at this level, cartilage joins the sphenethmoid to the prootic. Ventral to the frontoparietals in the mid-orbital region, the roof of the sphenethmoid splits to form the frontoparietal fontanelle (Fig. 101); the fontanelle extends posteriorly to the level of the optic foramen. The dense connective tissue which separates the sphenethmoid and frontoparietals is continuous across the frontoparietal fontanelle ventral to the frontoparietals. The anterior half of the fontanelle has a bony margin; the posterior part has a cartilaginous margin formed by the taenia tecti marginalis posterolaterally, and the tectum synoticum posteromedially.

The anterior end of the parasphenoid lies at the level of the orbitonasal foramen. The bone lies ventral to the sphenethmoid and prootic and forms a bony bridge of support for the neurocranial floor at the synchondrotic union of the sphenethmoid and prootic. The parasphenoid is separated from adjacent bones by connective tissue. Ventromedially, the parasphenoid bears a well developed odontoid structure.

The bursa angularis oris lies in the posterior part of the orbit between the pterygoid and maxillary bones. The position and size of the gland are like that described for *Tripriion petasatus*; however, the bursa seems to be better developed in *T. spatulatus*. It is encased in dense connective tissue. The gland lies parallel to the maxillary. It has a central lumen lined with cuboidal, ciliated epithelium; the surface of the lumen is folded into plicae. A longitudinal slit-like aperture connects the central lumen of the bursa with the oral cavity.

*The Otic and Occipital Regions.*—In dorsal view (Pl. 11a), the squamosal is an arcuate bone which extends posteriorly from the posterior edge of the orbit to the level of the occipital crest. The dorsal and dorsolateral surfaces of



FIGS. 100-101. Transverse sections through mid-region of skull of *Triprion spatulatus* (KU 86925): (100) level of orbitonasal foramen; (101) posterior level of orbit. Abbreviations: *b. ang. o.*, bursa angularis oris; *fpar.*, frontoparietal; *max.*, maxillary; *nas.*, nasal; *orbnas. f.*, orbitonasal foramen; *p. pal.*, pars palatina of maxillary; *post. max. proc.*, posterior maxillary process; *prsph.*, parasphenoid; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *spheth.*, sphenethmoid.

the head of the squamosal are completely involved in integumentary-cranial co-ossification. The anterior arm of the squamosal is robust and forms the posterior margin of the orbit; it terminates ventrally, adjacent to the maxillary at a level just posterior to the articulation of the pterygoid and maxillary. Dense connective tissue separates the anterior arm of the squamosal from the maxillary. The posterior arm of the squamosal is equally as robust as the anterior arm and extends nearly half the distance to the maxillary; there is a

heavy tendinous connection between the posterior end of the quadratojugal and the posterior arm of the squamosal. The ventral arm of the squamosal extends posteroventrally from the mid-point of the arc formed by the anterior and posterior arms of the squamosal; posteroventrally, the terminus lies between the quadratojugal and posterior ramus of the pterygoid.

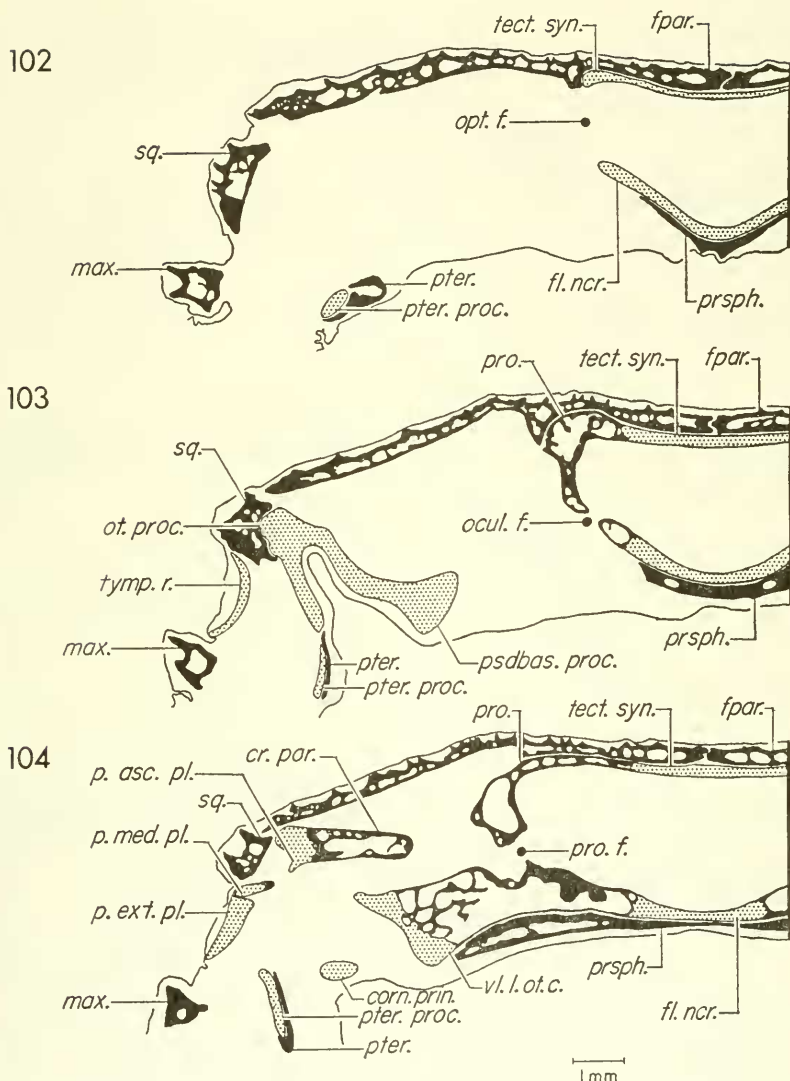
The pterygoid (Pl. 11b) is small. The anterior ramus attaches to the pars facialis of the maxillary, dorsal to the posterior end of the pars dentalis of the maxillary. The posterior ramus articulates with the ventral terminus of the squamosal. The medial ramus is reduced and does not articulate with the prootic.

The quadratojugal lies along the ventromedial surface of the maxillary. It terminates anteriorly, at the level of the articulation between the anterior arm of the squamosal and maxillary. Posteriorly, the quadratojugal extends beyond the end of the maxillary and lies adjacent to the ventral arm of the squamosal.

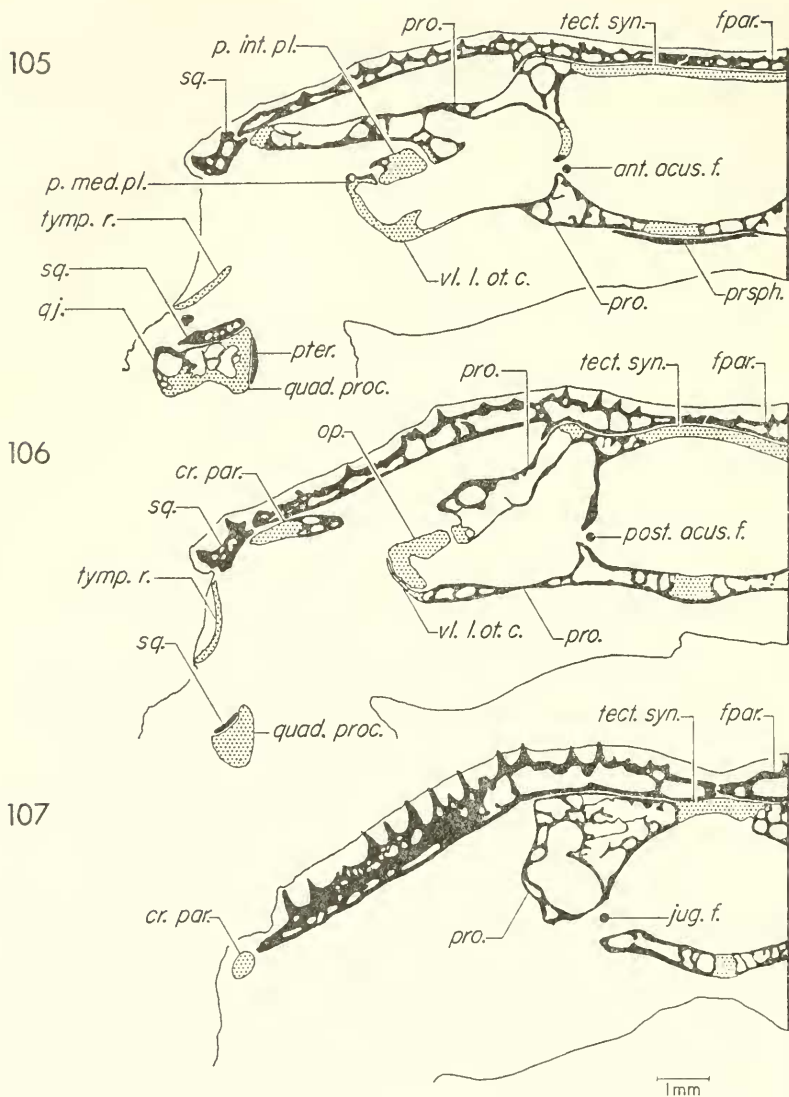
The anterior half of the optic foramen (Fig. 102) is cartilaginous; the posterior margins are bony and are formed by perichondral ossification of the prootic. The oculomotor foramen (Fig. 103) lies posteroventral to the optic foramen. The dorsal and posterior margins of the foramen are bony, whereas the anterior and anteroventral edges are cartilaginous. The trochlear foramen penetrates the lamina perpendicularis of the frontoparietal posterodorsal to the optic foramen. The large prootic foramen (Fig. 104) lies posterior to the oculomotor foramen and dorsal to the anteroventral edge of the otic capsule. The prootic foramen has a complete, bony margin. The anterior acoustic foramen (Fig. 105) is at the level of the pars interna plectri and has bony margins. The posterior acoustic foramen (Fig. 106), which lies at the level of the operculum, is separated from the anterior acoustic foramen by a narrow bridge of bone. The jugular foramen (Fig. 107) lies in bone posteroventral to the posterior acoustic foramen.

The anteriormost parts of the otic region are the pseudobasal and otic processes, which appear at the anterior level of the oculomotor foramen. The pseudobasal process lies ventrolateral to the neurocranium and expands medially in more posterior sections. The otic process appears initially as an oval cartilage lying medial to the anterior arm of the squamosal; it extends ventrally and fuses with the dorsolateral corner of the pseudobasal process at the posterior level of the oculomotor foramen. A short distance posterior to the latter fusion, the ventral part of the otic process divides; the medial part is fused to the pseudobasal process and the lateral part of the pterygoid process. Just anterior to the prootic foramen, the lateral part separates from the dorsal head of the otic process. The medial part of the otic process diverges from the pseudobasal process and becomes horizontally oriented as the crista parotica in posterior sections. At the same level as the separation of the otic and pseudobasal processes, the lateral part of the pseudobasal process diverges as the cornu principalis of the hyale.

At the posterior level of the ganglion prootic commune and the entry of the abducens nerve into the neurocranium, the pars ascendens plectri and pars externa plectri appear; both are cartilaginous. At the posterior margin of the prootic foramen, the pars ascendens plectri separates from the pars externa plectri and the pars media plectri appears; the latter is bony and attaches to the cartilaginous ventrolateral ledge of the otic capsule just anterior to the anterior acoustic foramen. The cartilaginous pars interna plectri appears at the



FIGS. 102-104. Transverse sections through skull of *Triprion spatulatus* (KU 86925) at levels of cranial nerve foramina: (102) level of optic foramen; (103) level of oculomotor foramen; (104) posterior level of prootic foramen. Abbreviations: *cr. par.*, crista parotica; *corn. prin.*, cornu principalis; *fl. ncr.*, floor of neurocranium; *fpar.*, frontoparietal; *max.*, maxillary; *ocul. f.*, oculomotor foramen; *opt. f.*, optic foramen; *ot. proc.*, otic process; *p. asc. pl.*, pars ascendens plectri; *p. ext. pl.*, pars externa plectri; *p. med. pl.*, pars media plectri; *pro.*, prootic; *pro. f.*, prootic foramen; *prsph.*, parasphenoid; *psdbas. proc.*, pseudobasal process; *pter.*, pterygoid; *pter. proc.*, pterygoid process; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring; *v. l. ot. c.*, ventrolateral ledge otic capsule.



FIGS. 105-107. Transverse sections through skull of *Triprion spatulatus* (KU 86925) at levels of cranial nerve foramina: (105) level of anterior acoustic foramen; (106) level of posterior acoustic foramen; (107) level of jugular foramen. Abbreviations: *ant. acus. f.*, anterior acoustic foramen; *cr. par.*, crista parotica; *fpar.*, frontoparietal; *jug. f.*, jugular foramen; *max.*, maxillary; *op.*, operculum; *p. int. pl.*, pars interna plectri; *post. acus. f.*, posterior acoustic foramen; *pro.*, prootic; *prsph.*, parasphenoid; *pter.*, pterygoid; *qj.*, quadratojugal; *quad. proc.*, quadrate process; *sq.*, squamosal; *tect. syn.*, tectum synoticum; *tymp. r.*, tympanic ring; *v. l. ot. c.*, ventrolateral ledge otic capsule.

level of the anterior acoustic foramen; the cartilaginous operculum is well developed at the posterior margin of the foramen. The pars interna plectri terminates at the level of the posterior acoustic foramen and the operculum closes the fenestra ovalis at the posterior margin of the posterior acoustic foramen.

At the posterior level of the optic foramen, the prootic is ossified only peripherally around the margin of the foramen. In subsequent sections, ossification increases in dorsomedial and ventromedial directions. At the posterior level of the prootic foramen, the medial part of the tectum synoticum and ventromedial part of the neurocranium, the distal edge of the crista parotica, and the ventrolateral ledge of the otic capsule are cartilaginous. Posteriorly, ossification increases in the floor of the neurocranium and decreases in the sides and roof. At the posterior level of the otic capsule, narrow dorsomedial and ventromedial strips of cartilage remain. The rest of the exoccipital region is bony.

*The Articular Region.*—Anterior to the articular region, Meckel's cartilage lies dorsolateral to the angulosplenic bone. Posteriorly, the cartilage enlarges and comes to lie in a dorsal position with respect to the angulosplenic; the latter assumes an arcuate shape in cross-section. The quadratojugal first appears in sections posterior to the union of the anterior pterygoid ramus with the maxillary. From an initial position ventromedial to the maxillary, the quadratojugal enlarges posteriorly and moves to a position medial to the maxillary as the latter decreases in size. Slightly anterior to the anterior acoustic foramen, the ossification of the quadratojugal invades the cartilage of the quadrate process. The quadratojugal remains separated from the pterygoid and squamosal throughout its length. At the level of the posterior acoustic foramen, the quadrate process is overlain by the posteroventral terminus of the ventral arm of the squamosal. The posterior end of Meckel's cartilage is attached ventrally to the quadrate process by connective tissue.

*Remarks.*—Little variation was noted in the skulls examined. The cranial differences noted between the subspecies of *Triprrion spatulatus* are minor and probably are indicative of individual variation, rather than subspecific differences. The skulls of mature females are much larger than those of mature males. In most males and in some small females, the sphenethmoid is exposed dorsally; in large females, the frontoparietals and nasals converge medially and completely cover the sphenethmoid.

Peters (1955:5) reported that "In this genus [*Triprrion spatulatus*] the labial shelf is made up of bony spines, . . . the group [of spines] on the tip of the snout is formed by the fusion of units from the two premaxillary bones." With reference to *Triprrion petasatus*, Peters stated in the same paper that "The fusion of the premaxillaries at the tip of the snout is complete . . ." Peters was unaware of the existence of the prenasal in *Triprrion* and thus misinterpreted the nature of the premaxillary.

#### VARIATION IN CRANIAL ELEMENTS IN CASQUE-HEADED, CO-OSSIFIED HYLIDS

The preceding morphological descriptions have shown that some areas and/or structures of the skull vary little from one genus to

another, whereas other cranial elements differ noticeably between closely related species. The purpose of the following account is to summarize and assay the kind and amount of morphological variation in individual cranial elements found in the genera of casque-headed, co-ossified hylids considered. Genera and species examined are: *Aparasphenodon bruno*i, *Corythomantis greeningi*, *Osteocephalus taurinus*, *Pternohyla dentata*, *Pternohyla fodiens*, *Trachycephalus jordani*, *Trachycephalus nigromaculatus*, *Tripriion petasatus*, *Tripriion spatulatus*, *Hyla septentrionalis*, *Hyla brunnea*, and *Hyla dominicensis*. Serial cross-sections of the heads were not available for *Hyla brunnea* and *H. dominicensis*; therefore these two species are not included in discussions of internal cranial elements. The accounts which follow are organized in the same order as each morphological description. The cranium has been divided into general areas which are treated in an anterior to posterior sequence. External bones associated with a particular area are discussed first and are followed by discussion of the appropriate internal bones and cartilages.

### The Olfactory Region (Including the Upper Jaw)

#### *External Dermal Bones*

*Prenasal*.—The prenasal is present in only two of the genera, *Aparasphenodon* and *Tripriion*. In both, the prenasal is dermal in origin, lies anterior to the premaxillary and nasal bones, and is co-ossified dorsally and smooth ventrally. Internally, the bone is hollow and contains the anterior parts of the alary processes of the premaxillaries and the anterior parts of the olfactory capsule. The prenasals of *Tripriion petasatus* and *T. spatulatus* differ from each other internally only slightly in the relationships of the prenasal septa and septa nasi. Externally, the prenasals of *T. petasatus* and *T. spatulatus* differ in patterns of co-ossification. Moreover, the prenasal of *T. spatulatus* bears a distinct dorsomedial ridge and a labial flange which turns down in lateral view, whereas the prenasal of *T. petasatus* lacks a distinct dorsomedial ridge and bears a labal flange which is dorsally concave in lateral view. The prenasal of *Aparasphenodon* differs from that of *Tripriion*; it lies between the anterior ends of the maxillaries, does not articulate with the premaxillaries posteriorly, and lacks a labial flange. Internally, the prenasal of *Aparasphenodon* lacks a prenasal septum.

*Internasal*.—The internasal is present only in *Pternohyla fodiens*. The relationship of this bone to the prenasal is unclear. The internasal is dermal and lies dorsal to the septum nasi between the external nares. In cross-section it resembles the posterodorsal part of the prenasal which extends between the external nares dorsal to the septum nasi. However, the two bones develop from different centers of ossification, and obviously differ functionally. The prenasal forms a bony anterior extension of the skull which encases and protects the anterior part of the nasal capsule, whereas the internasal seems

to act as a single anterior extension of the posterior nasal roofing bones. In *Corythomantis greeningi* the nasal extend anteriorly and anteroventrally and form a bony outgrowth similar in function and appearance to the prenasal. The modifications of the skulls of *Pternohyla*, *Triprion*, *Aparasphenodon*, and *Corythomantis* suggest a parallel trend among the casque-headed, co-ossified hylids to reinforce, protect and extend the anterior part of the skull. The minimal modification is that of *Pternohyla* with the addition of one, small, inconspicuous bone. *Aparasphenodon* and *Triprion* have amplified this trend with the addition of more elaborate bone, whereas *Corythomantis* has structured the same type of skull by modification of the nasal roofing bones.

*Premaxillary*.—Certain aspects of the premaxillary seem not to be subject to modification. The bone is always paired; the pair usually is separated medially by dense connective tissue and the bones are separated laterally from the maxillaries by dense connective tissue. Premaxillary dentition is invariably present. Some kind of alary process is present and acts as a bony abutment for the anterior end of the nasal capsule; the pars palatina and palatine process are present in greater or lesser degrees of development. The premaxillaries lie at the anterior end of the skull between the anterior ends of the maxillaries. In *Pternohyla* and *Aparasphenodon* the premaxillaries lie slightly recessed to the anterior ends of the maxillaries because of the anterior extension of the maxillaries.

The striking variation in the structure of the premaxillary almost exclusively involves various modifications of the alary process. The alary process is inclined anteriorly or posteriorly, or is nearly vertical in orientation. Alary processes vary in proportionate height and shape, and they are co-ossified or not. The alary processes are inclined anteriorly at approximately a 45-degree angle in *Triprion*, *Corythomantis*, and *Aparasphenodon*; these are the three genera characterized by anterior growth of dermal bone as a prenasal or an extension of the nasals. The alary processes of these frogs lie internal to the dermal bone at the anterior end of the skull. Consequently, the processes are not co-ossified; they are usually long, slender extensions of the pars dentalis of the premaxillary. In the remaining genera of frogs the alary processes are either vertically oriented or inclined slightly posteriorly. The degree of posterior inclination seems to be a function of the position of the anterior margin of the nasals or other dermal roofing bones. Thus, if the nasal projects forward between the external nares, dorsal to the level of the pars dentalis of the premaxillary, as it does in *Trachycephalus jordani* and *Osteocephalus taurinus*, the alary processes extend vertically from the pars dentalis to the level of the dorsal roofing bone. If the nasal terminates posterior to the level of the pars dentalis, as it does in *Hyla septentrionalis*, the alary processes are inclined posteriorly from the pars dentalis to the anterodorsal level of the dermal roofing bone.

The height of the alary processes varies principally in accordance with the projection and orientation of dermal roofing bones. Thus, the anteroventral projection of the nasals in *Trachycephalus jordani* results in proportionally shorter alary processes than those characteristic of *Hyla septentrionalis*. Lateral expansion of the alary processes is correlated with the occurrence of co-ossification of the alary processes in *Pternohyla fodiens*, *Trachycephalus jordani*, and *T. nigromaculatus*. This trend is least pronounced in *Pternohyla* in which the alary processes are laterally expended and slightly thickened by the develop-

ment of bony rugosities on the anterior surfaces of the processes. In *Trachycephalus nigromaculatus* the alary processes are completely co-ossified and expanded to articulate with one another medially and with the pars facialis of the maxillary laterally. The structure of the alary processes of *Trachycephalus nigromaculatus* is modified in *T. jordani* to include an anterior extension of bone into a small labial flange and a proliferation of bony spines dorsal to the flange.

*Prevomer.*—The prevomer of the casque-headed hylids is fully ossified. The anterior end lies dorsal to the pars palatina of either the premaxillary or the maxillary, or the articulation between the two bones. The prevomers are large, usually convergent medially, and all bear lateral wings which form the anterior, medial, and posteromedial margins of the internal nares. There is notable variation in the posterior dentigerous processes of the prevomer. Three genera are characterized by prevomers bearing small dentigerous processes. Those of *Tripriion* and *Corythomantis* are small and anteromedially inclined, whereas those of *Pternohyla* are small and posteromedially inclined. The prevomerine dentigerous processes of the other casque-headed hylids are larger, and either angular or curved. Those of *Hyla septentrionalis* and *Trachycephalus nigromaculatus* are slightly curved (see Table 1), whereas the dentigerous processes of *T. jordani* and *Hyla dominicensis* are more noticeably curved (see Table 1); the dentigerous processes of *Hyla brunnea* are very strongly curved (see Table 1). *Osteocephalus taurinus* has large, angular processes (see Table 1); those of *Aparasphenodon* are angular but smaller.

*Palatine.*—There is variation in the occurrence, the development, and the addition of ventral ridges and odontoid structures of the palatines of casque-headed hylids. The palatine is absent in *Corythomantis*, and reduced to an inconspicuous bone lying adjacent to the maxillary in *Tripriion petasatus*. In the other frogs, the palatines extend from the maxillaries to the sphenethmoid and vary from moderately robust to robust structures. There is a great deal of variation in the nature of ventral bony projections from the palatine. Some kind of bony ridge is present on all fully developed palatines. In its simplest state, the palatine ridge is low and smooth (*Hyla brunnea*). In other frogs (*Hyla dominicensis*, *Pternohyla dentata*, and *P. fodiens*), the ventral edge of the palatine ridge is slightly irregular. The palatine ridges of *Tripriion spatulatus*, *Osteocephalus*, *Trachycephalus nigromaculatus*, *T. jordani*, *Aparasphenodon*, and *Hyla septentrionalis* bear series of fine denticulate serrations and have therefore been classified as bearing odontoid structures. The palatines of *Hyla septentrionalis* are unique among the casque-headed hylids; each bone bears a row of tooth-like structures which protrude from the venter of the palatine posterior to the serrate palatine ridge.

*Nasal.*—There is little noteworthy variation among the nasals of the casque-headed hylids. The nasals converge medially and provide maximal dorsal coverage for the olfactory region. The culmination of this trend is the anterior development of the nasals in *Corythomantis*. The nasals provide a bony anterior margin for the orbit and articulate with the pars facialis of the maxillary at the anteroventral corner of the orbit. There is a complete articulation between the ventrolateral part of the nasal and the pars facialis of the maxillary in all the casque-headed hylids except *Trachycephalus nigromaculatus*, *Osteocephalus taurinus*, and *Pternohyla*. The dorsal configuration of the nasal surface is highly

variable. This is a function of the development of co-ossification; thus, frogs having the skin of the skull completely fused to the underlying cranial bones have heavier depositions of dermal bone. The pattern of bone deposition or sculpturing varies from irregular rugosities in partly casque-headed frogs, to reticulate or radial patterns of low bony ridges, and finally to reticulate or radial patterns of bony ridges which bear small spines in wholly casque-headed hylids.

*Maxillary.*—Variation in the maxillary is superficial, involving development of flanges along the outer surface, dermal surface configurations, extended anterior and posterior growth and the height of the pars facialis of the maxillary. The maxillaries of all the casque-headed hylids are alike in being robust and articulating anteriorly with the premaxillary and posteriorly with the quadratojugal; all have well developed partes faciale and partes palatinae. The partes faciale of all species, except *Pternohyla dentata*, *Osteocephalus taurinus*, and *Trachycephalus nigromaculatus* articulate along their dorsal margins with the nasals. In the latter species, the partes faciale articulate posterodorsally with the nasal to form a bony and complete anterior margin to the orbit. The pattern of co-ossification varies as described previously for the nasal. The nature of the development of labial flanges is a highly specific character and varies from a complete absence in *Hyla septentrionalis*, *Trachycephalus nigromaculatus*, and *Osteocephalus taurinus* to moderate development in *Corythomantis*, *Pternohyla*, *Aparasphenodon*, and *Trachycephalus jordani*, and finally, very extensive development in *Tripurion*. *Aparasphenodon* is distinguished by an anterior extension of the labial flange in front of the premaxillary; the pars dentalis terminates, as usual, adjacent to the pars dentalis of the premaxillary. Posteriorly, the maxillaries of all the casque-headed hylids are somewhat extended, forming a stronger articulation with the quadratojugal. This tendency is especially marked in *Corythomantis* in which the quadratojugal is reduced and the maxillary extended posteriorly to articulate with the quadrate process.

### Internal Bones and Cartilages and Associated Structures

*Superior Prenasal Cartilage.*—The superior prenasal cartilage is present in all casque-headed frogs for which sections were available. The cartilage lies adjacent to the posterodorsal surface of the alary process of the premaxillary and fuses posteriorly with the alary cartilage. The superior prenasal cartilage is more closely associated with the alary cartilage in those frogs having nearly vertical or posteriorly inclined alary processes of the premaxillaries. In *Pternohyla* the superior prenasal cartilage is a short rod of moderate diameter which extends from the alary process to the anteroventral part of the alary cartilage posteriorly (Pl. 12a). *Hyla septentrionalis* is similar except that the superior prenasal cartilage is longer and extends posterolaterally from the alary process to terminate at the anterior end of the alary process. The superior prenasal cartilage of *Osteocephalus taurinus* resembles that of *H. septentrionalis*, except that it is more massive. *Trachycephalus nigromaculatus* has the largest prenasal cartilage of the casque-headed hylids. The anterior end of the cartilage covers the dorsal half of the posterior surface of the alary process. The prenasal cartilage extends posterolaterally and dorsally and terminates at the anterior end of the alary process, which lies posteriorly adjacent to the lateral half of the superior prenasal cartilage.

In those frogs with anteriorly inclined alary processes of the premaxillaries, the superior prenasal cartilages are less well developed and not closely associated with the alary cartilage. The superior prenasal cartilages of *Aparasphenodon* and *Corythomantis greeningi* are depressed (Pl. 12b); they extend posterolaterally along the posterodorsal surface of the alary process. The anterior end of the alary cartilage is vertically oriented and fused to the lateral end of the prenasal cartilage. At the level of the posterior fusion of the alary cartilage with the solum nasi, the superior prenasal cartilage diverges posteroventrally from the alary cartilage and terminates. The superior prenasal cartilage of *Tripriion* is a compressed, laterally inclined rod (Pl. 12c), which extends posterolaterally from the posteromedial surface of the alary process. The dorsal part of the process thickens posteriorly and expands dorsally as the alary process.

*Alary Cartilage.*—There is only minor variation in the alary cartilages of the casque-headed hylids, since all the cartilages serve a similar function of laterally encasing the anterior end of the cavum principale. There is variation in the nature of the fusion of the superior prenasal cartilage and the alary cartilage as discussed previously. In all casque-headed, co-ossified hylids except *Pternohylla fodiens*, the alary cartilage is fused with the septum nasi (or solum nasi) anterior to the level of the cavum medium. In those frogs with nearly vertical alary processes and closely associated superior prenasal and alary cartilages (*Pternohylla dentata*, *Hyla septentrionalis*, *Trachycephalus nigromaculatus*, and *Osteocephalus taurinus*), the alary cartilage joins the septum nasi anterior to the development of the solum nasi. The latter is brought about either by the fusion of the dorsomedial or the ventromedial corner of the alary cartilage with the septum nasi. In frogs having anteriorly inclined alary processes (*Aparasphenodon*, *Corythomantis*, and *Tripriion*), the ventromedial corner of the alary cartilage fuses with the solum nasi. Posterior to the appearance of the cavum medium, the alary cartilage is typically arcuate in cross-section. It reaches its maximum size anterior to the anterior margin of the external nares. Posterior to the latter level, the alary cartilage gradually diminishes in size and terminates.

*Inferior Prenasal Cartilage.*—The anterior end of the inferior prenasal cartilage lies adjacent to the posteroventral surface of the alary process of the premaxillary. From the alary process, the inferior prenasal cartilage curves posterodorsally and then extends posteromedially to fuse with the ventral surface of the solum nasi. The anterior end of the inferior prenasal cartilage lies at approximately the same level in all the casque-headed hylids examined. However, there is some variation in the level at which the inferior prenasal cartilage fuses with the solum. The cartilage is shortest in *Hyla septentrionalis* and *Trachycephalus nigromaculatus*; it fuses with the solum nasi at a level just anterior to the formation of the nasolacrimal duct and the opening of the cavum principale into the cavum medium. In *Corythomantis*, fusion of the inferior prenasal cartilage occurs at the level of the nasolacrimal duct formation and the opening of the cavum principale into the cavum medium. In *Pternohylla* and *Osteocephalus taurinus*, fusion occurs slightly posterior to the latter level. *Tripriion* and *Aparasphenodon* differ from all other casque-headed hylids in having inferior prenasal cartilages which fuse with the solum nasi posteriorly at the level of the planum terminale and the confluence between the cavum principale and cavum inferius.

*Nasal Cavities.*—There are always three nasal cavities (the cava principale, medium, and inferius) in the olfactory capsules of the casque-headed hylids. The cavities show some minor variations in the positions and occurrence of recesses but on the whole are remarkably similar in structure. *Hyla septentrionalis* is exceptional in having the anterior ends of the nasal cavities aligned in a reverse sequence as compared with the other frogs, in which, in an anterior to posterior direction, the appearance of the cavum principale is followed by the cavum medium and finally by the cavum inferius, whereas the reverse is true in *H. septentrionalis*. *Pternohyla* and *Tripriion* differ from the other frogs by having a bifurcate cavum principale; the anterior end of the cavum in these genera is divided into medial and lateral recesses by a thin septum. In the majority of the casque-headed species, the cavum inferius bears only an antero-lateral recess. The cava inferius of *Aparasphenodon* and *Tripriion* bear an anteromedial recess of equal size to the anterolateral recess.

*Tectum Nasi, Septum Nasi, and Solum Nasi.*—A detailed report of the variation in these and associated structures such as the lamina inferior and superior, crista intermedia, planum antorbitale, planum terminale, crista subnasalis, cartilago obliquus, and the anterior and posterior maxillary processes would yield a variety of small differences. The significance of such variation is doubtful and of questionable value in a study like this one. It is important to note that with the exception of the crista subnasalis, all of these structures are present in the casque-headed hylids and show no major variation in form or relative positions. Endochondral ossification occurs only in the septum nasi and solum nasi. The anterior limits of ossification in the septum nasi lie at approximately the anterior level of the olfactory eminence. The solum nasi ossifies slightly posterior, at the anterior level of the internal nares. Both elements are completely ossified at the posterior level of the internal nares. The septum nasi is synosteotically united with the sphenethmoid posteriorly.

*Septomaxillary.*—The septomaxillaries of the casque-headed hylids have certain structural characteristics in common. All are basically "U"-shaped bones, which are oriented in a horizontal plane with the closed end lying anterior. There is a dorsal ramus arising from the lateral branch of the U-shaped structure, and a ventral ramus attaching in some fashion to the same branch. The anterior end of the septomaxillary always lies dorsal to the cavum medium. The posterior separation of the medial and lateral branches of the septomaxillary accommodates the confluence of the cava principale and medium; the dorsal ramus provides lateral support, and the medial branch forms medial support for the canal joining the two cava. The ventral ramus lies beneath the cavum medium; it fuses with the dorsal and lateral rami just posterior to the lateral divergence of the nasolacrimal duct from the cavum medium.

There are two basic variations, both involving the ventral ramus, on the structural plan described above. In *Pternohyla* and *Tripriion*, the ventral ramus attaches only to the posteroventral part of the lateral branch of the septomaxillary (Type I septomaxillary, Fig. 108a). In all other genera, the ventral ramus is laterally joined to the anterior end of the septomaxillary (Type II septomaxillary, Fig. 108b); posteriorly, the ventral ramus fuses with the lateral branch of the septomaxillary in the same way that it does in *Pternohyla* and *Tripriion*.

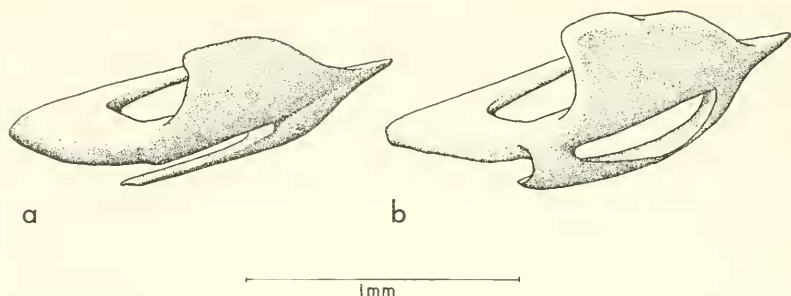


FIG. 108. Septomaxillaries of casque-headed, co-ossified hylids. Anterolateral views: (a) Type I septomaxillary, (b) Type II septomaxillary.

### Relationship of Internal to External Structure

Superficial examination of the external aspects of the skull show that there is a great amount of morphological variation in the dermal bones of the olfactory region. This striking variation, unfortunately, does little to reveal the kind of associated internal changes that have occurred concomitant to external modification. Some of the minor variations in the superior and inferior prenasal cartilages and the associated types of premaxillaries have been discussed previously. The rest of the olfactory structures have been shown to be surprisingly uniform.

The entire olfactory region can be conveniently divided into two regions. The first and most anterior of these includes the septomaxillaries, the external nares, the cavum medium, the anterior end of the cavum principale, and the cavum inferius posterior to the posterolateral recess of the cavum at the level of the planum terminale. The superior and inferior prenasal cartilages lie anterior to the anterior unit and brace it against the alary process of the premaxillary. The planum terminale marks the posterior border of this part of the olfactory region. The second part of the olfactory capsule consists of the posterior parts of the cavum principale, the lateral recess of the cavum inferius, the olfactory eminence, and the internal nares. This region is bordered posteriorly by the palatine bones and the transition zone of the planum antorbitale, which marks the anterior end of the sphenethmoid and orbital region.

Whereas only minor variation was noted in the separate elements of the anterior part of the olfactory region, there is considerable variation in the position of the anterior unit with relation to the external bones. Among those frogs lacking labial flanges and having vertical or posteriorly inclined alary processes of the premaxillaries, the position of the anterior unit of the olfactory region is determined anteriorly by the position of the alary processes. In *Osteocephalus taurinus* the alary processes are inclined slightly anteriorly; the anterior end of the cavum principale lies near the base of the alary process anterior to the level of the pars dentalis of the premaxillary. The alary processes are inclined only slightly posteriorly in *Trachycephalus*, and the anterior end of the cavum principale lies dorsal to the posterior part of the pars dentalis of the premaxillary. The posterior inclination of the alary processes is especially marked in *Pterohyla fodiens*; in this species the anterior end of the cavum

principale lies dorsal to the terminal level of the palatine process of the premaxillary.

In *Tripriion*, *Aparasphenodon*, and *Corythomantis* an entirely different situation prevails with respect to the positions of the anterior and posterior units of the olfactory capsule. The planum terminale, or the posterior border of the anterior unit, lies dorsal to the level of the pars dentalis of the premaxillary. The posterior unit terminates as usual at the planum antorbitale just anterior to the orbit. In the account of the development of the skull of *Tripriion petasatus*, it was shown that the young frog has a blunt snout. Further development results in the anterior growth of the nasals and consequently an anterior shift of the external nares, which are bordered posteriorly by the anterior ends of the nasals. An anterior rotation of the premaxillaries occurs concurrent with the latter change. Since the external nares are closely allied morphologically with the anterior ends of the cava principale, it seems reasonable to conclude that anterior migration of the external nares causes the forward shift of the anterior unit of the olfactory region. The posterior unit of these frogs is proportionately much longer than the same area of the remaining casque-headed species. Thus, it is apparent that anterior growth of the posterior region, coordinated with the anterior extension of the overlying nasals, forces the anterior part of the nasal capsule forward. The pressure of the anterior growth and movement of the olfactory capsule is probably responsible for the anterior rotation of the alary processes of the premaxillaries in these three genera.

### The Sphenethmoid and Associated Bones

*Frontoparietal*.—The frontoparietal is extremely well developed in all of the casque-headed species. The bone articulates anteriorly with the nasal and the dermal sphenethmoid, if the latter is present. The frontoparietals articulate medially throughout their lengths, thereby eliminating the occurrence of a dorsally exposed frontoparietal fontanelle. Variation in the frontoparietal primarily consists of lateral, posterolateral, and posterior extension of the bone. The frontoparietal is the least developed in *Osteocephalus taurinus*, which has only a narrow supraorbital flange extending along the outer edge of the bone. *Pternohyala dentata* has added a posterolateral process to the frontoparietal; this process is an extension of the supraorbital flange around the posterior end of the orbit. In the rest of the casque-headed hylids, the frontoparietal forms a broad supraorbital flange and terminates laterally at the level of the squamosal, and posteriorly near the posterior margin of the crista parotica of the prootic. The frontoparietal articulates laterally with the anterior and/or posterior arms of the squamosal in *Hyla septentrionalis*, *H. dominicensis*, *Pternohyala fodiens*, *Tripriion petasatus*, and *T. spatulatus*. In *Hyla brunnea*, *Corythomantis*, *Aparasphenodon*, *Trachycephalus nigromaculatus*, and *T. jordani*, the frontoparietal lacks a lateral articulation. The frontoparietal bears a prominent transverse occipital crest in *Tripriion*. The crest is moderately developed in *Trachycephalus jordani*, *Corythomantis*, and *Aparasphenodon*, but absent in the remaining species and genera. The most obvious single source of variation in the frontoparietal is in the configuration of the dorsal surface. The latter is a highly specific character and varies in the manner described for the nasal.

*Dermal Sphenethmoid*.—A dermal sphenethmoid occurs in all the casque-headed hylids examined except *Pternohyla* and *Triprion spatulatus*. The bone is approximately diamond-shaped, or triangular with an anterior apex. The dermal sphenethmoid lies in the centrally depressed region of the skull between the paired nasals anteriorly and the frontoparietal posteriorly. It is always confluent with the underlying endochondral sphenethmoid as described for *Hyla septentrionalis* (Trueb, 1966).

The dermal sphenethmoid is laid down at the same time that the other dermal roofing bones are co-ossifying and represents the co-ossification of the dorsally exposed part of a cartilage replacement bone. The development and co-ossification of the dermal sphenethmoid allows the dorsal surface of the skull to be configured into a uniform and complete pattern. The presence of the dermal sphenethmoid provides bony margins with which the nasals and frontoparietals articulate anteriorly and posteriorly, thereby strengthening the skull.

*Sphenethmoid*.—The endochondral sphenethmoid of all species of casque-headed hylids are overlapped dorsally by the nasals and frontoparietals. In most species, dorsal coverage is completed by the addition of the dermal sphenethmoid centrally or the convergence of the posteromedial corners of the nasals and anteromedial corners of the frontoparietals. *Pternohyla* is distinctive in having a dorsally exposed sphenethmoid which is smooth and not co-ossified. Ventrally, there is little variation in the sphenethmoid; all are ossified dorsal to the prevomers, and heavily ossified posteriorly. The sphenethmoid of *Triprion petasatus* differs from those of the remaining genera and species in its bony, ventrolateral articulation with the nasal. The latter is probably a structural compensation for the reduced palatines, which do not articulate with the sphenethmoid.

Internally, there is very little variation in the structure of the sphenethmoid. Anteriorly, the bone is ossified, except for the anterolateral wings ventral to the nasals. The margins of the orbitonasal foramen are bony. The roof of the sphenethmoid splits ventral to the frontoparietals, forming a frontoparietal fontanelle in all species. The anterior end of the fontanelle corresponds approximately with the anterior margins of the frontoparietals. The anterior margins of the fontanelle are bony, whereas the posterior margins are formed in cartilage by the taenia tecti marginali laterally and the tectum synoticum posteriorly at the level of the optic foramen. The frontoparietal fontanelle is completely roofed by the overlying frontoparietals in all species.

*Parasphenoid*.—The parasphenoid lies ventral to the sphenethmoid and prootic, and forms a bony bridge of support for the floor of the neurocranium between the levels of the ossified parts of the two bones. The anterior end of the parasphenoid is usually acuminate and lies slightly posterior to the level of the palatines; posteriorly, the parasphenoid terminates at the exoccipital. The parasphenoid is smooth and edentate in most of the species of casque-headed hylids (*Hyla dominicensis*, *H. brunnea*, *H. septentrionalis*, *Pternohyla*, *Aparasphenodon*, and *Corythomantis*). *Trachycephalus nigromaculatus* has a single, smooth longitudinal ridge, and *Osteocephalus taurinus* has a small proliferation of two or three odontoids located ventromedially just anterior to the base of the parasphenoid. *Trachycephalus jordani* and *Triprion petasatus* have long,

serrate, medial ridges, and *Tripriion spatulatus* a wide, longitudinally oriented, proliferation of small denticules.

There is some variation in the basolateral wings of the parasphenoid, which probably conforms to, and reflects variation in, the configuration of the underlying prootic. The wings slope posterolaterally in *Hyla dominicensis*, *H. brunnea*, *H. septentrionalis*, and *Osteocephalus taurinus*; in the remaining species the wings are perpendicularly oriented to the longitudinal axis of the parasphenoid. The wings are moderately slender in all species, except *Tripriion spatulatus*, in which they are wide. The basal part of the parasphenoid is smooth in all species, except *Aparasphenodon* and *Corythomantis*, in which the parasphenoids bear prominent anteroventral-projecting, transverse ridges at the level of the anterior margins of the basolateral wings of the parasphenoid.

## The Orbital, Otic, and Occipital Regions

### *External Dermal Bones*

*Squamosal*.—The squamosal is robust in all species of casque-headed hylids. The head of the squamosal (the anterior and posterior arms) articulates with the ossified crista parotica medially. In *Hyla dominicensis*, *H. septentrionalis*, and *Tripriion*, the head of the squamosal also articulates with the posterolateral margin of the frontoparietal. The anterior arm of the squamosal articulates with the maxillary in *Tripriion* and usually in *Hyla septentrionalis*. The anterior arm of the squamosal in *Pternohyla* articulates with the pterygoid and maxillary. The arm lies dorsally adjacent to, but does not articulate with, the maxillary in *Hyla dominicensis*, *Trachycephalus nigromaculatus*, *T. jordani*, and *Corythomantis*. In the remaining species (*Osteocephalus taurinus*, *Aparasphenodon*, and *Hyla brunnea*) the anterior arm is narrowly to widely separated from the maxillary. The anterior and posterior arms of the squamosal are involved in integumentary-cranial co-ossification in all but two species, *Hyla brunnea* and *Osteocephalus taurinus*; these species are characterized by the poorest development of co-ossification and the shortest anterior squamosal arms among the casque-headed hylids.

*Pterygoid*.—Variation in the pterygoid involves the length of the anterior ramus and the presence or absence of a bony articulation between the medial ramus of the pterygoid and the ventrolateral ledge of the otic capsule. The anterior ramus is the longest in *Pternohyla* in which it terminates between the levels of the palatine and the orbitonasal foramen. In *Trachycephalus nigromaculatus*, *T. jordani*, *Aparasphenodon*, and *Corythomantis*, the end of the anterior ramus lies slightly posterior to the level of the orbitonasal foramen. The remaining species (*Hyla septentrionalis*, *H. brunnea*, *H. dominicensis*, *Osteocephalus taurinus*, and *Tripriion*) have short anterior rami which terminate at approximately the mid-level of the orbit. The medial ramus of the pterygoid bears a strong articulation with the prootic in *Corythomantis*, *Trachycephalus jordani*, *Osteocephalus taurinus*, *Pternohyla fodiens*, *Hyla septentrionalis*, and *H. brunnea*. The articulation is absent in the other species.

Cursory inspection of the architecture of an anuran skull suggests that three primary elements (the palatine, pterygoid, and squamosal) share the important function of securing and bracing the maxillary against the neurocranium. The palatine constitutes a brace between the anterior part of the maxillary and

sphenethmoid. Similarly, the pterygoid braces the mid- and posterior parts of the upper jaw against the prootic. The squamosal acts to secure the position of the maxillary by articulating with the prootic dorsally (the crista parotica) and the maxillary ventrally. *Pternohyla fodiens* is unique among the casque-headed hylids in having the maximal and fully articulated states of development of all three of these bones. Thus, the palatine is robust and articulates with the maxillary and sphenethmoid; the pterygoid bears a long anterior ramus which articulates with the maxillary from a level slightly posterior to the palatine, posterior to the level of divergence of the pterygoid from the maxillary. The medial ramus of the pterygoid articulates with the prootic, and the anterior arm of the squamosal articulates with the pterygoid and pars facialis of the maxillary.

In the other casque-headed hylids, the relative development of the anterior arm of the squamosal, the anterior and medial rami of the pterygoid, and the palatine seems to be compensatory or interdependent in nature. For example, in a group of moderately-ossified hylids composed of *Osteocephalus taurinus*, *Hyla brunnea*, and *H. dominicensis*, the palatines are moderately well developed, and the anterior rami of the pterygoids terminate at the mid-level of the orbit. The anterior arm of the squamosal is widely separated from the maxillary in *Osteocephalus taurinus* and *Hyla brunnea*, but the medial ramus of the pterygoid bears a strong articulation with the prootic. A converse arrangement occurs in *Hyla dominicensis*, in which the anterior arm of the squamosal lies dorsally adjacent to the maxillary and articulates with the latter by means of dense connective tissue, but the medial ramus of the pterygoid does not articulate with the prootic. Both *Aparasphenodon* and *Corythomantis* lack firm articulations between the squamosals and maxillaries and have lengthy articulating surfaces between the anterior rami of the pterygoids and the maxillaries. *Aparasphenodon* has a robust palatine but lacks an articulation between the pterygoid and prootic, whereas *Corythomantis* lacks a palatine but bears a pterygoid-prootic articulation. A parallel situation exists in *Triprion*, which is characterized by the absence of an articulation between the pterygoid and prootic. In *Triprion petasatus*, the palatine is reduced to a seemingly non-functional sliver of bone adjacent to the maxillary, whereas the articulation between the anterior arm of the squamosal and maxillary is strong. In *Triprion spatulatus*, the latter articulation is much weaker, but the palatine is better developed.

*Quadratojugal*.—The quadratojugal varies little in its occurrence in the casque-headed hylids. The bone lies posteromedial to the maxillary and articulates throughout its length with the maxillary. Posteriorly the ossification of the quadratojugal invades the cartilage of the quadrate process. *Corythomantis* is distinctive among the casque-headed hylids by having a greatly reduced quadratojugal.

*Exoccipital-Prootic-Frontoparietal*.—There is little or no variation in the relationship of these three elements. The frontoparietal lies dorsally adjacent to the exoccipital and prootic and is always separated from the latter bones by a thin layer of dense connective tissue. The prootic and exoccipital are fused; the juncture of the two bones is indistinguishable.

## Internal Bones and Cartilages

*Cranial Nerve Foramina.*—Variation in the cranial nerve foramina is minor and involves the positions of the trochlear foramen, the oculomotor foramen with respect to the optic and prootic foramina, and the number of acoustic foramina. The trochlear foramen is usually located in the dorsomedial part of the optic foramen; the trochlear and optic nerves are separated by connective tissue. In *Corythomantis* the foramen lies in the posterodorsal part of the optic foramen, and in *Pternohyla* and *Tripriion* it is located dorsomedial to the optic foramen in the lamina perpendicularis of the frontoparietal. In all species examined, except *Hyla septentrionalis* and *Tripriion*, the oculomotor foramen lies slightly anterior to the prootic foramen. In *Hyla septentrionalis*, the oculomotor foramen lies just posterior to the optic foramen and is widely separated from the posterior prootic foramen, whereas in *Tripriion* the oculomotor foramen lies approximately equidistant between the levels of the optic and prootic foramina. *Aparasphenodon* and *Pternohyla fodiens* are unique among the casque-headed hylids in having only one large acoustic foramen instead of two smaller foramina (the anterior acoustic and posterior acoustic foramina).

*Otic Region.*—The basic pattern of the otic region seems to vary only in two major respects. The first concerns the relative positions of the otic and pseudobasal processes, and the second, the orientation of the columella. In *Tripriion* and *Pternohyla*, the anterior ends of the otic and pseudobasal processes lie at approximately the same level; the elements fuse a short distance posterior to their appearance. The anterior end of the otic process lies far anterior to the pseudobasal process in *Osteocephalus taurinus*. In the remaining species, the anterior end of the pseudobasal process lies anterior to the otic process; the elements are separated by a relatively short distance in *Corythomantis*, *Aparasphenodon*, and *Hyla septentrionalis*, and by a great distance in *Trachycephalus nigromaculatus*.

Three types of columellae occur in the casque-headed hylids. The columellae are oriented anterolaterally or posterolaterally. Among those directed anterolaterally, the columellae of *Trachycephalus nigromaculatus*, *Osteocephalus taurinus*, and *Pternohyla* are curved, whereas those of *Tripriion spatulatus*, *Hyla septentrionalis*, and *Corythomantis* are straight. The columellae of *Tripriion petasatus* and *Aparasphenodon* are oriented posteriolaterally and are straight.

There is considerable variation in the relative positions of the structures of the otic capsule and the cranial nerve foramina. This is most striking anteriorly. Thus, among those frogs in which the oculomotor foramen lies only slightly anterior to the prootic foramen, the anterior end of the pseudobasal process lies at the level of the optic foramen in *Trachycephalus nigromaculatus*, at the posterior edge of the optic foramen in *Pternohyla*, and between the levels of the oculomotor and prootic foramen in *Aparasphenodon* and *Corythomantis*. The anterior end of the otic process of *Osteocephalus taurinus* lies at approximately the same level as the pseudobasal process of *Aparasphenodon* and *Corythomantis*. The oculomotor foramen of *Hyla septentrionalis* occupies a position just posterior to the optic foramen; the anterior end of the otic capsule lies slightly posterior to the oculomotor foramen. In *Tripriion petasatus* and *T. spatulatus* the oculomotor foramen lies equidistant between the optic and prootic foramina and the anterior ends of the otic capsules lie at the level of the optic foramen

and just posterior to the optic foramen, respectively. As a rule, the posterior edge of the operculum lies between the levels of the posterior acoustic and jugular foramina, or in the case of *Aparasphenodon*, anterior to the jugular foramen. *Osteocephalus taurinus* is exceptional; the operculum terminates posterior to the jugular foramen.

At this time, it is impossible to evaluate the data presented above. Obvious difference in sizes and proportions of the otic capsule occur. Specifically, the otic region appears to occupy a much greater area in *Tripriion* and *Trachycephalus* than in *Corythomantis* and *Aparasphenodon*, for example. But such conclusions are tenuous without a definite frame of reference.

The degree of ossification of the otic region is remarkably consistent in the casque-headed hylids. The tectum synoticum is cartilaginous; posteriorly some ossification invades the roof of the neurocranium, but ossification is never complete. Similarly, the floor of the neurocranium retains a ventromedial strip of cartilage varying in width depending on the species. The sides of the neurocranium are bony, and with rare exceptions the cranial nerve foramina are bordered by bone. The otic capsules are well ossified. Cartilage usually forms the ventrolateral ledge and to varying degrees the posterodorsal part of the otic capsule. Ossification of the columellae and cristae paroticae is consistent. The distal tip of the crista parotica, which is encased in the head of the squamosal, is cartilaginous. Medial to the squamosal, the crista parotica is ossified. The pars externa plectri, pars ascendens plectri, pars interna plectri and operculum are cartilaginous, whereas the pars media plectri is ossified.

### *Bursa Angularis Oris*

The bursa angularis oris is present in varying states of development in all casque-headed hylids. It is the most highly organized in *Osteocephalus taurinus*, *Corythomantis*, and *Aparasphenodon*. In these species, the bursa is a long, tubular structure, encased in connective tissue, and having a central lumen and distinct aperture into the oral cavity. *Hyla septentrionalis*, *Trachycephalus nigromaculatus*, and *Tripriion spatulatus* have bursae that are somewhat less well developed. The gland is long and encased in connective tissue, but does not bear a central lumen anterior to the aperture into the oral cavity. The bursa is very poorly developed in *Tripriion petasatus* and *Pternohyla*. The gland is loosely encapsulated in connective tissue. It bears no central lumen and is situated along the surface of the oral cavity adjacent to the maxillary.

### The Articular Region

With the single exception of *Corythomantis*, the articular regions of the casque-headed genera are the same and composed of six elements, the quadrate process, the ventral arm of the squamosal, the posterior ramus of the pterygoid, the quadratojugal, Meckel's cartilage, and the angulosplenial. The pterygoid process fuses posteriorly with the quadrate process. The posterior ramus of the pterygoid lies medially adjacent to the quadrate process; the ventral arm of the squamosal is dorsally adjacent to it, and the quadratojugal lies laterally adjacent. The three bony elements surrounding the quadrate process remain separate. The ossification of the quadratojugal invades the cartilage of the quadrate process posteriorly; the posterior terminus of this ossification marks the end of the quadratojugal. Posterior to the quadratojugal, the remaining

bony elements terminate, leaving the quadrate process and Meckel's cartilage as the most posterior elements of the articular region. *Corythomantis* departs from this pattern; the maxillary invests the quadratojugal laterally, and lies adjacent to the quadrate process posterior to the terminus of the quadratojugal.

#### EVOLUTIONARY RELATIONSHIPS OF THE CASQUE-HEADED, CO-OSSIFIED HYLIDS

Hylid frogs are represented by approximately 30 genera and some 450 species (see Goin, 1961, for the most recent synopsis of the Hylidae). All the genera are represented in the New World except *Nyctimantis* of the Papuan region. By far the greatest diversity of hylids occurs in the New World tropics. The distribution of the casque-headed, co-ossified hylids is restricted to the New World tropics with the single exception of the northern part of the range of *Pternohyla fodiens*. The geographical distribution of the casque-headed, co-ossified hylids is summarized as follows: *Pternohyla*—low and moderate elevations from southwestern United States (Arizona) to Michoacán, México; *Triprion*—the Pacific lowlands from Sinaloa to Oaxaca, México, the Yucatan Peninsula of México, and northern Guatemala; *Hyla septentrionalis* group—the West Indies and southern Florida of the United States; *Trachycephalus*—the Pacific slopes of Colombia and Ecuador, and the lowlands of eastern Brazil southward to Argentina; *Osteocephalus*—the upper Amazon Basin in Brazil, Peru, and Ecuador; *Corythomantis*—the xeric region of northeastern Brazil; *Aparasphenodon*—the costal region of southeastern Brazil and the upper Orinoco Basin of Venezuela.

Savage (1966) pointed out that the Middle American and South American herpetological assemblages are distinct, having been separated throughout much of the Cenozoic by seaways. It is obvious, from the numbers of kinds of frogs and their diversities, that the primary differentiation of the hylids occurred within the South American or Neotropical assemblage, whereas the Mesoamerican or Central American assemblage was a secondary center of diversification. *Triprion* and *Pternohyla* are members of the latter fauna. *Aparasphenodon*, *Corythomantis*, *Trachycephalus*, and *Osteocephalus* belong to the first, or Neotropical, group. The history of the West Indian hylids is somewhat problematic. The most recent work on the relationships of the Antillean faunas relates them to South American forms and therefore makes the Antillean faunas a northeastern extension of the Neotropical assemblage. My own observations suggest that the West Indian *Hyla septentrionalis* group is more closely allied with South American forms than any other known group.

### The *Hyla septentrionalis* Group

In attempting to ferret out the relationships of a specialized group of frogs, one seeks a less specialized animal sharing basic morphological features and, ideally, a distributional pattern which links it geographically and/or chronologically with the more specialized members. The *Hyla septentrionalis* group presents problems from the outset because there are no frogs currently inhabiting the Antilles which could have given rise to this group, or clearly descend from an ancestral type.

The osteology of the *Hyla septentrionalis* group is very similar to that of another specialized genus, *Osteocephalus*; but these two groups of tree frogs differ in one essential morphological character (Table 1). *Osteocephalus* is characterized by paired, lateral vocal sacs which lie behind the angles of the jaws, whereas frogs of the *Hyla septentrionalis* group have single, median, subgular vocal sacs. The same character divergence differentiates this group from *Trachycephalus*. It is obvious, on the basis of general appearance alone, that the *Hyla septentrionalis* group is not related to *Aparasphenodon*, *Corythomantis*, *Pternohyla*, or *Triprion*.

There is a group of large, generalized tree frogs in South America which have single, median, subgular vocal sacs, and show osteological affinities with the *Hyla septentrionalis* group. These are the frogs of the *Hyla boans* group (*faber*, *boans*, and *rosenbergi*). Although principally restricted to the Amazonian lowlands or the Pacific slopes of South America, the ranges of two members of this group extend northward into Central America. *Hyla rosenbergi* is found along the Pacific slopes of Central America as far north as southern Costa Rica, and *Hyla boans* inhabits the Caribbean lowlands of eastern Panamá. The skulls of this group are large and broader than long. The maxillaries and premaxillaries are robust. The pars facialis of the maxillary is extensive but poorly ossified anteriorly; posteriorly, the pars facialis articulates with the maxillary process of the nasal, forming a bony anterior orbital margin. The dermal roofing bones are not greatly expanded, consequently the olfactory region is poorly covered laterally, and a frontoparietal fontanelle is exposed posteromedially. The ossification of the sphenethmoid is greatly expanded. In *Hyla boans* the sphenethmoid, at its widest level (at the level of the palatines), comprises more than one-third the width of the skull. The bone diminishes rapidly in width posteriorly. The quadratojugal is robust and articulates firmly with the maxillary. The squamosal arch is incomplete, but in all species the squamosal bears a broad articulation with the crista parotica. The palatines are moderately developed and edentate, although they do bear well defined ventral ridges. The prevomers are large and characterized by massive dentigerous processes which are angular and curved (see Table 1). The parasphenoids are well developed and edentate. The pterygoids are robust and fully articulated.

The evidence for an alliance between the *Hyla boans* group and the *Hyla septentrionalis* group is inconclusive. Although this conclusion is based partly on negative evidence and largely on speculation, I think it is at least reasonable to assume tentatively that the West Indian hylids evolved from a generalized, mainland South American stock. With respect to the former, there are no tree frogs currently known in Central America which seem to be related to the *Hyla septentrionalis* group. This fact limits the choice to a South American group. The current interpretation of the colonization of the Greater Antilles

favors over-water dispersal from the mainland of South America and lower Central America (Simpson, 1956; Darlington, 1957; King, 1962). If the latter is in fact the case, then distributionally the *Hyla boans* group or its progenitors is a plausible candidate for waif dispersal to the Greater Antilles.

On the basis of osteology, two evolutionary lines are evident within the *Hyla septentrionalis* group. *Hyla vasta* is found on Hispaniola, and has been observed to deposit eggs on the ground as well as in bromeliads (Noble, 1923). *Hyla dominicensis* and *H. septentrionalis* are obviously closely related and constitute one phyletic line. Both species have developed greatly expanded dermal roofing bones and co-ossification. *Hyla septentrionalis* is probably the more advanced of the two species; the dermal ossification of *H. septentrionalis* is more extensive, the nasals overlap the sphenethmoid farther posteriorly, and the squamosal arch is complete. The breeding habits of both species are generalized. *Hyla dominicensis* breeds in streams and ponds in the forest and has been noted to utilize cisterns (Mertens, 1939). Similar observations to the latter were made for *Hyla septentrionalis* by Duellman and Schwartz (1958). *Hyla dominicensis* is found on Hispaniola, whereas *H. septentrionalis* ranges throughout Cuba, the Isle of Pines, the Bahamas, and north to southern Florida. The distributional and morphological evidence suggest that *Hyla septentrionalis* and *H. dominicensis* could have evolved from a *vasta*-like ancestor which first colonized Hispaniola. Subsequent adaptive radiation probably produced a casque-headed frog on Hispaniola ancestral to *Hyla septentrionalis* and *H. dominicensis*. Later dispersal of this form to Cuba could reasonably have resulted in the evolution of *Hyla septentrionalis* which has subsequently dispersed throughout islands nearby Cuba and the adjacent North American mainland.

*Hyla brunnea* and *H. lichenata* represent the second phyletic line. Both have developed extensive dermal ossification and have similarly diverged from the *H. septentrionalis*-*H. dominicensis* line by a modification of the nasals. The nasals project farther forward and bear more distinct canthal ridges. By comparison with *Hyla septentrionalis* and *H. dominicensis*, the breeding habits of these frogs are specialized; they are only known to deposit their eggs in bromeliads (Myers, 1950). Both *Hyla brunnea* and *H. lichenata* are endemic to Jamaica. This would seem to suggest that an ancestral form, probably casque-headed, migrated from Hispaniola to Jamaica and subsequently produced these two species.

### *Aparasphenodon* and *Corythomantis*

Although it is generally agreed that *Aparasphenodon* and *Corythomantis* are closely related, there is no consensus of opinion concerning their relationships with the other casque-headed, co-ossified hylids. Rivero (1961) was under the erroneous impression that *Aparasphenodon* possessed paired, lateral vocal sacs; thus, he related *Aparasphenodon* to *Trachycephalus*. Miranda-Ribeiro (1920) proposed that *Aparasphenodon* represented a subsection of *Diaglena* (*Tripriion spatulatus*); later, Myers (1942) suggested that *Aparasphenodon* and *Corythomantis* were members of a natural group also including *Tetrapriion* (*Trachycephalus jordani*), *Tripriion*, and *Diaglena* (*Tripriion spatulatus*). Miranda-Ribeiro (1920) noted the similarity between *Aparasphenodon* and *Tripriion spatulatus*, but excluded *Tripriion petasatus* because it possessed verti-

cal pupils. Myers (1942) did not regard the latter character to be important, and based his conclusions on zoogeographic evidence and the similarity of cranial-casque patterns.

*Aparasphenodon* and *Corythomantis* share a number of characteristics which evidence a close relationship between them and clearly separate the two genera from the other casque-headed hylids (Table I). The skulls are narrow anteriorly and long. The labial flanges are absent or poorly developed; therefore the snouts are acuminate by comparison with the other casque-headed hylids. The parasphenoids are poorly developed and edentate. *Aparasphenodon* and *Corythomantis* are obviously distinct from the Antillean casque-headed hylids on the bases of size and general appearance. Furthermore, the skulls of *Aparasphenodon* and *Corythomantis* are characterized by labial flanges, prominent patterns of co-ossification, the presence of a prenasal or anterior extension of the nasals, anteriorly concave canthal ridges, and poorly developed parasphenoids. The single, median, subgular vocal sacs of these two genera distinguish them from the South American *Trachycephalus* and *Osteocephalus*. Superficial examination seems to suggest that *Aparasphenodon* and *Corythomantis* are closely related to the geographically distant *Triprrion*. However, there are several important differences between the South American genera and the Middle American *Triprrion*. The parasphenoid of *Triprrion* is robust and bears odontoid structures. The labial flanges of *Triprrion* are very well developed. The surface configuration of the dermal bones of *Triprrion* is delicate and in low relief, whereas that of *Aparasphenodon* and *Corythomantis* is coarse by comparison. The quadratojugal tends to be reduced in *Aparasphenodon* and *Corythomantis*; the bone is robust in *Triprrion*. The otic region is anteriorly expanded in *Triprrion* and not expanded in *Aparasphenodon* and *Corythomantis*. The cavum principale is anteriorly bifurcate in *Triprrion* and single in *Aparasphenodon* and *Corythomantis*. The latter genera have Type II septomaxillaries, whereas *Triprrion* has a Type I septomaxillary.

In the descriptive account of *Corythomantis greeningi*, attention was drawn to the striking resemblance of this species to a member of the *Hyla rubra* group. This is a group of small to moderate-sized hylids, containing about 24 species (León, in press). These frogs are widespread from lowland México to Argentina and are most diverse in southeastern Brazil (Cochran, 1955). Members of this group have a single, median, subgular vocal sac. According to León, the members of this group are characterized by the following osteological features: prevomerine teeth on transverse ridges; skull generally longer than wide; nasals large (length more than 40 per cent total length of skull); quadratojugal slender, always joined to maxillary by bony suture; crista parotica slender and short; columella delicate and spatulate; squamosal arch incomplete; and prevomer, premaxillary, and maxillary teeth present. The cranial characters in the *Hyla rubra* group are highly variable and show a trend towards reduction of ossification. Unlike other small hylids, the reduction principally involves the prootic region, prevomers, palatines, pterygoids, and parasphenoid. The members of the *Hyla rubra* group retain a well-ossified sphenethmoid and dermal roofing bones.

*Hyla boulengeri* (Fig. 109a) is one of the more completely ossified members of the *Hyla rubra* group. The skull is depressed and the snout attenuate. The nasals are extremely large, the sphenethmoid well ossified, and the frontoparietals convergent medially. The palatines, parasphenoid, prootic, and prevomers are

well developed, and the latter articulate with the premaxillaries anteriorly. The medial ramus of the pterygoid articulates with the prootic. By comparison, the cranial elements of another member of the *H. rubra* group, *Hyla staufferi* (Fig. 109b), are greatly reduced in ossification. Like *Hyla boulengeri*, the skull is depressed, the nasal large, and the sphenethmoid well ossified. The frontoparietals are not completely convergent medially; thus, a small frontoparietal

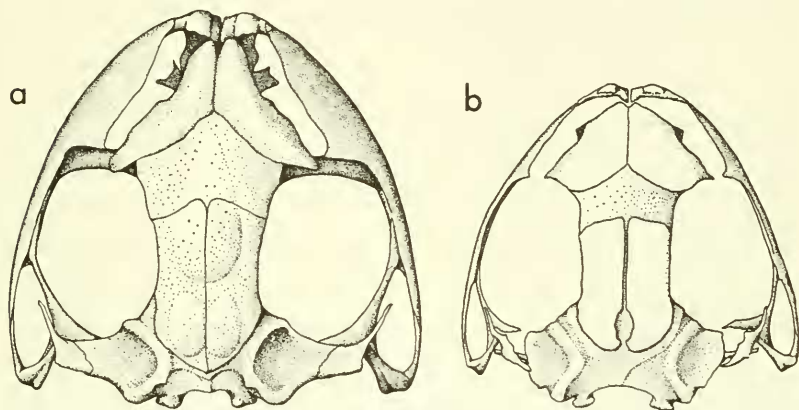


FIG. 109. Dorsal views of the skulls of (a) *Hyla boulengeri* (KU 104352), and (b) *Hyla staufferi* (KU 60614).  $\times 3.3$ .

fontanelle is exposed. The prevomers are small and do not articulate with the maxillaries or premaxillaries. The parasphenoid and prootic are only moderately developed. The medial ramus of the pterygoid does not articulate with the prootic, and the palatines are absent. The "*Hyla rubra*" (Fig. 71a) from Jacareacanga, Pará, Brazil, has a skull somewhat intermediate between those of *Hyla boulengeri* and *H. staufferi*. The pterygoid articulates with the prootic, but the parasphenoid and palatines are very poorly developed.

The similarity between the "*Hyla rubra*" from Jacareacanga and *Corythomantis greeningi* suggests that the latter represents a phyletic line derived from the *Hyla rubra* group. Although *Corythomantis* has increased ossification of dermal roofing bones, other elements are markedly reduced or absent. Among the most important are the absence of the palatine and the reduced parasphenoid and quadratojugal. *Aparasphenodon* shows slightly different evolutionary trends, and it has a greater amount of dermal ossification than *Corythomantis*. The former has a prenasal, whereas in *Corythomantis* the anterior extension of the nasals fulfills the same functional requirement. The dentigerous processes of the prevomers are massive and angled in *Aparasphenodon*, whereas they are small and transverse in *Corythomantis*. The palatines are reduced but not absent in *Aparasphenodon*, and the medial ramus of the pterygoid does not articulate with the prootic as it does in *Corythomantis*. These differences in cranial characters, together with the larger size of *Aparasphenodon*, are the features by which the genera are separated. The similarity of cranial structure suggests a common ancestor for the two genera, but the differences preclude the evolution of *Aparasphenodon* from *Corythomantis*.

The widespread geographical and ecological distribution of the *Hyla rubra* group in South America, the range of osteological characters possessed by the group, and the similarity of the general cranial structure and vocal sacs to those of *Aparasphenodon* and *Corythomantis* suggests that they were derived from the *Hyla rubra* group. *Corythomantis* and *Aparasphenodon brunoi* are restricted to the subhumid environments of the *caatinga* of northeastern Brazil and the *restinga*, the coastal lowlands from Espirito Santo to Guaynabara, of southeastern Brazil, respectively. The single specimen of *Aparasphenodon venezolana* is from the savanna-scrub region of Venezuela. At least as recently as the late Pliocene, subhumid environments (open woodland and savanna) were more widespread in eastern South America than they are today; possibly these environments were continuous from the cerrado of southern Brazil to the Caribbean (Ducke and Black, 1953; Savage, 1955). Probably *Corythomantis* and *Aparasphenodon* had a common ancestor, which was at least partly casque-headed and inhabited these subhumid areas. This ancestral stock differentiated into a stock of small frogs restricted to the xeric *caatinga* and another stock of larger frogs that was widespread in subhumid savannas and/or open woodlands. The development of the present-day distribution of rainforest in the Amazon Basin in the Pleistocene separated the latter stock, *Aparasphenodon*, into Venezuelan and Brazilian populations; the former developed into *A. venezolana* and the latter into *A. brunoi*. The development of the forests further isolated the *Corythomantis* stock in the *caatinga*, where it developed into *C. greeningi*.

### *Osteocephalus* and *Trachycephalus*

*Osteocephalus* and *Trachycephalus* are moderately large South American tree frogs which are distinguished by two characters from all other New World hylids. The crania of these genera are casqued and co-ossified, and the vocal sacs are paired, lateral, and located behind the angles of the jaws. The latter character separates *Osteocephalus* and *Trachycephalus* from the other casque-headed, co-ossified hylids (Table I), and the former character differentiates these two genera from *Phrynohyas*, the only other hylid with paired, lateral vocal sacs. Relatively little is known about *Osteocephalus*. Goin (1961) assigned eight or ten species to this genus. I have examined only *O. taurinus* and *O. lepricuri* (*O. lepricuri* is virtually indistinguishable from *O. taurinus* osteologically) and hesitate to include any other species in the genus. *Osteocephalus* is purported to range from the Guyanas and northern Brazil to Colombia (Lutz and Kloss, 1952). Bokermann (1964) reported on some field observations of *O. taurinus* made in Rondonia Territory, near Marmelo, Brazil. There is considerably more information available on *Trachycephalus*, an inhabitant of disjunct, sub-humid environments. At least four species are assigned to this genus; these are *T. jordani* from the Pacific lowlands of Ecuador and southern Colombia, *T. atlas* from the eastern coast and probably the *caatinga* of Brazil (Bokermann, 1966), *T. nigromaculatus* from southeastern Brazil (Lutz, 1954; Cochran, 1955), and *T. siemersi* from Uruguay and northeastern Argentina.

Lutz and Kloss (1952:655) alluded to a relationship between *Osteocephalus* and *Trachycephalus* in their statement that *O. taurinus* “. . . seems intermediate between *Hyla* and *Trachycephalus*.” A strong case can be postulated for a close relationship between *Osteocephalus* and *Trachycephalus* on the bases of the similar structure of the vocal sacs and their osteological character-

istics. The skulls of both genera are longer than broad and the snouts rounded. The dermal roofing bones are expanded and co-ossification is partial or entire. The canthal ridges are distinct and not anteriorly concave. Prenasal and internasal bones are absent. The prevomers are large and fully ossified. The dentigerous processes of the prevomers are massive and curved. The palatines are well developed and bear odontoids. Both genera have Type II septomaxillaries (Fig. 108b). The parasphenoids are well developed and bear some type of odontoid structure. The cranial nerve foramina are arranged in the same spatial sequence.

There are obvious differences between the skulls of *Osteocephalus* and *Trachycephalus*, but these are principally the result of a marked evolutionary trend toward increased dermal ossification from *Osteocephalus* to *Trachycephalus*. The snout of *Osteocephalus* is less rounded (tending toward a truncate shape; compare plates 5a and 6a) than that of *Trachycephalus*. The alary processes of the premaxillaries of *Trachycephalus* are expanded and co-ossified; the addition of bone anteriorly imparts a more rounded shape to the snout. The nasal and pars facialis of the maxillary have increased in size and tend to articulate with one another, forming a complete or nearly complete lateral cover to the olfactory region in *Trachycephalus*. Proliferation of frontoparietal ossification results in a wider supraorbital shelf (and consequently a greater interorbital width), extension of the frontoparietal over the crista parotica to the medial margin of the squamosal, and the development of a posterior, transverse occipital crest in *Trachycephalus*. The surface configuration of the dermal roofing bones is prominently developed in *Trachycephalus*, whereas in *Osteocephalus* it is inconspicuous. The pattern of co-ossification in *Osteocephalus* is a reticulate network formed of low, bony ridges which is reminiscent of the pattern established during the early development of co-ossification in *Triprion petasatus*. This seems to suggest that *Osteocephalus* represents a rather primitive state in the phyletic development of co-ossification. By comparison with *Trachycephalus*, the squamosal of *Osteocephalus* is poorly developed. It is not involved in co-ossification and the anterior arm extends only about half the distance to the maxillary. The squamosal arch is essentially complete in *Trachycephalus*. The anterior arm of the squamosal does not articulate firmly with the maxillary, but it lies dorsally adjacent to the maxillary. Correlative with the strengthened squamosal arch, the pterygoid of *Trachycephalus* has undergone modification. The medial ramus of the pterygoid does not articulate with the prootic as it does in *Osteocephalus*, but the articulation of the anterior ramus is stronger. The anterior end of the anterior ramus of the pterygoid extends forward to a level just posterior to the trochlear foramen in *Trachycephalus*, whereas the anterior ramus terminates at the mid-level of the orbit in *Osteocephalus*.

The parasphenoid of *Osteocephalus* is characterized by slender basal wings which slope posterolaterally. The basal wings of the parasphenoid in *Trachycephalus* are wider by comparison and transversely oriented. The shapes of the basal parts of the parasphenoids conform to differences in the prootic bones and otic capsules overlying them. In view of this, it is interesting to note that the otic capsule of *Osteocephalus* lies between the levels of the oculomotor and jugular foramina. In *Trachycephalus*, the otic capsule occupies the area between the optic and jugular foramina (*T. nigromaculatus*) or the area from the anterior level of the oculomotor foramen to the jugular foramen (*T. jordani*);

thus, the otic capsule of *Trachycephalus* is somewhat expanded anteriorly in comparison with *Osteocephalus*.

The structural variation of the bursa angularis oris in *Osteocephalus* as compared with *Trachycephalus* is probably indicative of the reduction of this gland in more advanced forms. The bursa is very well developed in *Osteocephalus*, in which it is long, tubular, encased in a connective tissue capsule, and characterized by a distinct aperture into the oral cavity. In *Trachycephalus* the bursa is similarly developed but distinguished by a relatively poorly developed central lumen and connective tissue capsule.

The trend towards increased ossification is evident within *Trachycephalus*. *Trachycephalus nigromaculatus* (Pl. 6a) is the least specialized member of the genus. I have examined photographs (Bokermann, 1966: Figs. 3-4, p. 123) of the skull of *T. atlas* from Bahia, Brazil; this species is obviously closely related to the more southern *T. nigromaculatus*. In the description of the species, Bokermann (1966) reported the following osteological differences between *T. nigromaculatus* and *T. atlas*: (1) the interorbital space of *T. atlas* is wider; (2) the loreal region is more vertical; and (3) the frontoparietals project farther posteriorly and are more heavily sculptured in *T. atlas*. In terms of increased ossification these differences may be accounted for by (1) lateral extension of the frontoparietal into a wider supraorbital shelf; (2) proliferation of the nasal and pars facialis of the maxillary, extending the length of the articulation of the two bones; and (3) posterior expansion of the frontoparietals and a general proliferation of surface rugosities characteristic of increased co-ossification. The same three evolutionary trends have been further exploited in *T. jordani* (Pl. 7a) on the west coast of South America. *Trachycephalus jordani* is further distinguished from the eastern members of the genus by a development of shallow maxillary and premaxillary flanges. An anteromedial notch between the alary processes of the premaxillaries is characteristic of *T. atlas* and *T. nigromaculatus*. A similar notch is present in *T. jordani* but is reduced because of the proliferation of dermal bone on the alary processes. Examination of the internal structure of the anterior end of the skull of *T. jordani* shows that the bony posterior surface of the alary processes have been secondarily resorbed, forming cavities within the projecting anterior ossification of the premaxillaries. The nasal capsule has moved forward to occupy this shallow cavity, foreshadowing slightly the condition characteristic of *Triprrion*, *Aparasphenodon*, and *Corythomantis*.

Earlier in this discussion, attention was drawn to a third genus of hylid frogs, *Phrynohyas*, which possesses paired, lateral vocal sacs like those of *Trachycephalus* and *Osteocephalus*. *Phrynohyas* consists of at least six species (*hebes*, *imitatrix*, *ingens*, *quadrangularum*, *mesophea*, and *venulosa*); the genus is widespread in the lowlands of South America along the Caribbean coast, in the Orinoco basin, the Guianas, the Amazon Basin west to Bolivia and Ecuador and south to Paraguay and northern Argentina. The genus is also known from the islands of Trinidad and Tobago, and the west coast of Ecuador. One species, *Phrynohyas venulosa*, ranges north from South America along the Pacific coast of Panamá and Costa Rica, and thence northward along both the Pacific and Caribbean coasts to Tamaulipas and Sinaloa, México (Duellman, 1956). *Phrynohyas venulosa* is the best known and most widely distributed member of the genus and like the others is morphologically generalized.

The skull of *Phrynohyas venulosa* closely resembles that of *Osteocephalus*; this was discussed at the end of the descriptive account of the latter. Some of the more important features are worth recounting here. The anterior dermal roofing bones are expanded. The maxillaries and premaxillaries are robust. The squamosal arch is incomplete. The prevomers are large, and their dentigerous processes are massive and curved. The palatines are well developed. The pterygoid is fully articulated. The terminus of the anterior arm of the pterygoid lies at the mid-level of the orbit. The basal wings of the parasphenoid are slender and slope posterolaterally. Fundamentally, the skulls of *Phrynohyas venulosa* and *Osteocephalus taurinus* are the same. All but one of the osteological characters which distinguish *Osteocephalus* from *Phrynohyas* can be evolved by proliferation of dermal bone in the same way that *Trachycephalus* was derived from *Osteocephalus*. The single character which separates *Phrynohyas* and *Osteocephalus* is the condition of the septomaxillary. *Phrynohyas* has a Type I septomaxillary, which, at the present stage of investigation, is known to occur only in this genus, *Smilisca*, *Pternohyla*, and *Triprion*. *Osteocephalus*, *Trachycephalus*, *Hyla rubra* and *H. lanciformis* of South America, *Pseudacris* of North America, and the other genera of casque-headed, co-ossified hylids are characterized by a Type II septomaxillary. The consequences of this single character divergence of the septomaxillary are difficult to evaluate in view of the other outstanding similarities among *Phrynohyas*, *Osteocephalus*, and *Trachycephalus*. The widespread distribution, and the generalized habits and morphology of *Phrynohyas* would seem to indicate that its members represent a logical choice for modern descendants of a progenitor which gave rise to a single phyletic line of casque-headed frogs beginning with *Osteocephalus* and terminating with *Trachycephalus jordani*.

It is possible that the condition of the septomaxillary in *Phrynonhyas* represents an evolutionary link with another generalized stock of hylids, *Smilisca*. This genus is widespread in Central America; two members are present in north-western South America. *Smilisca* is postulated to be an autochthonous Middle American group (Duellman and Trueb, 1966). Like *Phrynohyas venulosa*, the skull of *Smilisca baudini*, the most widespread and generalized member of the genus, is unspecialized. The species inhabits lowlands and shows few specializations of habits. The vocal sacs are bilobed and subgular, a condition thought by Duellman (1966) to be less advanced than the paired, lateral vocal sacs of *Phrynohyas*.

It can be hypothesized that *Phrynohyas* and *Smilisca* arose from a single ancestral stock, which probably inhabited the lowlands and had a weakly bilobed vocal sac and a Type I septomaxillary. This stock was separated into Central American and South American components by the Panamanian Portal throughout much of the Cenozoic; these components evolved into *Smilisca* and *Phrynohyas*, respectively.

It has been hypothesized that the extensive tropical rain forest in the Amazon Basin probably did not reach its present distribution until late Pleistocene (Duellman, 1958). Earlier in the Cenozoic, much of the basin was an epeiric sea in which there was a deposition of sediments from the erosion of the Andes (Oliveira, 1956). The savanna and open woodlands that now exists in south-central Brazil were probably continuous with those in northern South America in the Pliocene and probably into the Pleistocene, as evidenced by isolated patches of this habitat throughout the eastern part of the Amazon Basin (Ducke

and Black, 1953, and Veloso, 1947). If this was the case, the prototype of *Phrynohyas* must have adapted to subhumid conditions. The habits of *Phrynohyas venulosa* were summarized by Duellman (1956), and indicate adaptation to existence in subhumid environments. The activity of the frog is controlled by seasonal rainfall. The frogs take day-time and dry-season refuge in bromeliads, banana plants, and occasionally palms. *Phrynohyas* is an inhabitant of gallery forests, savannas, and rain forests in areas where rainfall is strongly seasonal. If the ancestral *Phrynohyas* stock was similarly adapted to subhumid environments, it could have dispersed southward along the north-western coast of South America, eastward through the northern scrub forest, savanna, and open woodlands, and thence southward toward eastern Bolivia and northern Paraguay. Temporally and geographically, this distributional pattern is compatible with that suggested for the *Leptodeira annulata* stock by Duellman (1958).

It seems feasible to postulate that during this extended period of subhumid conditions, an evolutionary trend toward increased ossification within the widespread *Phrynohyas* stock resulted in the development of the casque-headed genera *Osteocephalus* and *Trachycephalus*. Like *Phrynohyas*, *Osteocephalus* is a forest inhabitant, principally in areas of seasonal rainfall. *Trachycephalus*, on the other hand, is an inhabitant of more arid areas, usually characterized by low forest and scrub vegetation and marked by prolonged dry seasons. It is possible that prior to the uplift of the Andes and the development of rain forests in the Amazon Basin, a subhumid habitat was distributed across the South American continent and occupied by a casque-headed hylid intermediate between *Osteocephalus* and *Trachycephalus*. After the uplift of the Andes and the development of tropical rain forests in the Amazon Basin, a *Trachycephalus* stock was divided into two isolated units in the eastern and western coastal regions of South America. The western component gave rise to *T. jordani*, and the eastern component to a frog like *T. nigromaculatus*. The latter was probably distributed along the coastal region of South America from northeastern Brazil to northeastern Argentina and later differentiated into a southern species (*T. siemersi*), a central species (*T. nigromaculatus*), and a northern species (*T. atlas*).

### *Triprion* and *Pternohyla*

Considerable attention has been devoted to the two Middle American genera of casque-headed hylids, *Triprion* and *Pternohyla*. *Triprion* has been associated most often with *Trachycephalus jordani* (Rivero, 1961; Smith, 1957; Myers, 1942; and Peters, 1955), on the bases of the shapes of the skulls and the nature of odontoids present. Smith (1957) included *Pternohyla* in this group. Although they are not similar in superficial appearance, several characters relate *Pternohyla* and *Triprion*. Both genera have bilobed, or median, subgular vocal sacs, Type I septomaxillaries, and cava principalae which are bifurcate anteriorly (Table 1). These characters separate *Pternohyla* and *Triprion* from the Antillean casque-headed hylids (single, median, subgular vocal sac, Type II septomaxillary, non-bifurcate cavum principale), *Aparasphenodon* and *Corythomantis* (single, median, subgular vocal sac, Type II septomaxillary, non-bifurcate cavum principale), and *Osteocephalus* and *Trachycephalus* (paired, lateral vocal sacs, Type II septomaxillary, non-bifurcate cavum principale).

*Pternohyla* and *Triprrion* share the same three characters with *Smilisca baudini*, a moderate-sized, generalized hylid which ranges throughout the Pacific and Atlantic lowlands of México from southern Sonora and the Río Grande embayment of Texas southward to Costa Rica. Duellman and Trueb (1966) have hypothesized an evolutionary history of the genus *Smilisca*. According to their account, the prototype of *Smilisca* lived in the mesic tropical environment of the eastern part of the Central American Peninsula. Earlier this stock diverged from the stock which gave rise to *Phrynohyas*, *Osteocephalus*, and *Trachycephalus* in South America. In the late Miocene the ancestral stock of the *Smilisca baudini* group dispersed northwestward into upper Central America and then into southern México. The subsequent elevation of mountains in late Miocene or Pliocene resulted in the development of subhumid lowland areas. The *Smilisca* stock inhabiting the Pacific lowland areas during this period is postulated to have given rise to *Smilisca baudini*. It is reasonable to assume that this stock also produced a casque-headed phyletic line which was adapted to the more xeric environments along the Pacific lowlands. Subsequently, this group, the prototype of *Triprrion*, dispersed across the Isthmus of Tehuantepec and into the Yucatan Peninsula. This dispersal probably took place during a glacial period of the Pleistocene when, due to fluctuations in the water table, semi-arid environments were continuous at times from the Pacific lowlands across the isthmus to the Gulf lowlands. During interglacial periods of higher water tables, the lowlands . . . were more restricted (Duellman, 1960). The restriction of suitable subhumid environments through the subsequent development of wet forests on the Atlantic side of the isthmus resulted in the isolation of populations of the *Triprrion* stock on the Pacific lowlands of México and in the Yucatan Peninsula. The former gave rise to *Triprrion spatulatus*, a somewhat less specialized species than *Triprrion petasatus*, which inhabits the arid portions of the Yucatan Peninsula and also exists as relict populations in the savannas in El Petén, Guatemala. *Triprrion petasatus* differs from *T. spatulatus* in having a dermal sphenethmoid, a reduced palatine, a very poorly developed bursa angularis oris, and a bilobed vocal sac. The vocal sac of *T. spatulatus* is single and median. Although *T. spatulatus* lacks a dermal sphenethmoid, the nasals and frontoparietals converge medially, dorsal to the sphenethmoid; this condition is probably functionally equivalent to the development of the dermal sphenethmoid. However, *T. spatulatus* has only a moderately developed palatine and bursa angularis oris, characters which are further reduced in *T. petasatus*.

In the descriptive account of *Pternohyla*, it was shown that structurally *Smilisca baudini* is very similar to both species of *Pternohyla*. Moreover, it was demonstrated that one form could be derived from another by increased dermal ossification in the following sequence: *Smilisca baudini*—*Pternohyla dentata*—*Pternohyla fodiens*. The structure of the skull of *Pternohyla*, unlike that of the other casque-headed hylids, shows adaptations reflecting the fossorial habits of the genus. In both species, the crania are depressed. Although solidly roofed, the skulls lack distinct labial flanges. The palatines are robust, the squamosal arches complete, and the pterygoids fully articulated. Further specialization is evident in *Pternohyla fodiens* which has developed an internasal and more extensive dermal roofing bones, and has incorporated the two acoustic foramina into one large acoustic foramen.

The resemblances between *Triprion* and *Smilisca baudini* involve the septomaxillaries, the olfactory capsule, the prevomerine dentigerous processes, and the structure of the vocal sac. *Pternohyla* shares the same characters with *Smilisca baudini* as does *Triprion*. Additionally it has been demonstrated that the shape of the skulls of *Pternohyla* and *Smilisca* are similar and that *Pternohyla* differs principally from *S. baudini* in the presence of co-ossification, further expansion of dermal roofing bones, and addition of the internasal in *P. fodiens*. The dermal roofing bones are much less expanded in *Pternohyla* than in *Triprion*. *Pternohyla* lacks a dermal sphenethmoid and the nasals and frontoparietals are not completely convergent dorsal to the sphenethmoid. Co-ossification of the skull of *Pternohyla* is not complete, and the pattern of co-ossification forms a poorly organized reticulate network reminiscent of the pattern formed in the early development of co-ossification in *Triprion*. These morphological data suggest that *Pternohyla* may have been more recently derived from the *Smilisca* stock than *Triprion*. Furthermore, the structure of the skull of *Pternohyla* seems to reflect adaptations of the frogs to fossorial habits. A *Smilisca baudini*-like ancestor probably gave rise to a fossorial stock in response to the increased aridity during the Pleistocene. The fossorial ancestor was probably widespread over the Pacific lowlands of México and very similar in appearance to *Pternohyla dentata*. Further evolution in this stock resulted in the appearance of the more advanced *Pternohyla fodiens*. *Pternohyla dentata* is known only from the upper Río Santiago Basin on the Mexican Plateau, and probably represents a relict population of the ancestral stock of *P. fodiens*.

#### CONCLUSIONS

Geographical and morphological evidence indicates that the casque-headed, co-ossified condition has arisen at least six times within the Hyliidae. Thus, five phyletic lines gave rise separately to *Triprion*, *Pternohyla*, *Trachycephalus* and *Osteocephalus*, *Aparasphenodon* and *Corythomantis*, the *Hyla septentrionalis* group, and the gastrothecine hylids. The first five groups are treated in this study. The last group, consisting of *Gastrotheca*, *Flectonotus*, *Anotheca*, *Nyctimantis*, and *Amphignathodon*, is discussed only briefly. The gastrothecine hylids seem to bear little evolutionary relevance to the other groups. Moreover, they are represented by so few specimens that it is impossible to complete a satisfactory morphological study of them at the present time.

An hypothesized phyletic arrangement of the other five groups of casque-headed, co-ossified hylids is shown in Figure 110. The vertical scale represents geological time. The horizontal scale is divided into the three geographical areas in which the evolution of the casque-headed forms occurred. The heavy horizontal bars intersecting phyletic lines in the Pliocene and Pleistocene represent the development of casques and co-ossification. These morpho-

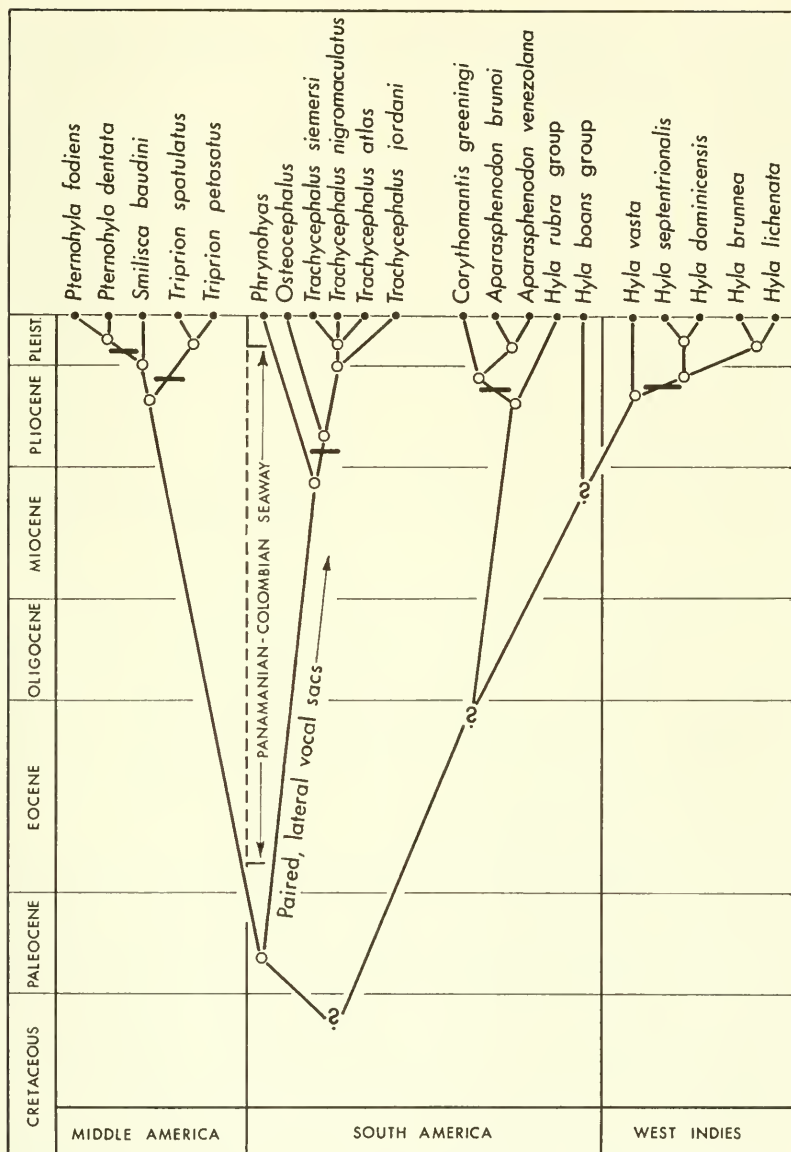


FIG. 110. Proposed phylogenetic relationships of the casque-headed, co-ossified hylids. Vertical scale represents geological periods. Vertical exaggeration of the Pleistocene is  $\times 2$ . The horizontal scale shows the geographical areas in which evolution of the casque-headed hylids took place. Open circles represent frogs which no longer exist, whereas closed circles are frogs presently known and named at the top of the figure. Heavy horizontal bars intersecting phyletic lines indicate the development of casques and co-ossification.

logical specializations are apparently associated with the widespread occurrence of subhumid environments in the latter part of the Pliocene and the Pleistocene.

Three principal problems have confused the previous systematic interpretations of the casque-headed, co-ossified hylids. Several of the species are poorly represented in collections, and until now, no one person has had the advantage of studying examples of each genus. Previous workers have attributed too much reliability to the taxonomic value of the presence or absence of odontoids on the palatines and parasphenoid. This has been shown to be a highly labile character which is closely associated with sexual and ontogenetic variation. And finally, the striking parallelism which has been involved in the evolution of these frogs has been overlooked.

The single most obvious quality shared by the casque-headed, co-ossified hylids is the similarity of their environments. Thus, those genera which utilize the most similar habitats look the most alike externally. Taking all of these points into consideration, the following arrangement is possible.

1. *Triprion*, *Aparasphenodon*, *Corythomantis*, and *Trachycephalus*.—These four genera are characterized by long skulls, labial flanges, sculpturing of dermal roofing bones, and the addition of dermal bone at the anterior end of the skull. All inhabit xeric environments where terrestrial bromeliads and tree holes often afford the only suitable moist shelters. *Trachycephalus*, the least specialized of the group, is also found in less xeric environments where it utilizes trees for shelter.

2. *Osteocephalus*, *Hyla septentrionalis*, *Hyla brumnea*, and *Hyla dominicensis*.—These species are very similar in general appearance. They are large, and the skulls are only slightly broader than long. They lack labial flanges, prominent sculpturing, and addition of dermal bone at the anterior end of the skull. All are characterized by inconspicuous dermal sculpturing and the presence of a dermal sphenethmoid. These frogs are inhabitants of forests, which although wet, are characterized by highly seasonal rainfall.

3. *Pternohyla*.—The frogs in this genus are unique in possessing a depressed skull in which few, if any, signs of internal reduction are evident. One species has an internasal bone. The genus is an inhabitant of xeric areas, where it utilizes terrestrial burrows for shelter.

Unfortunately the above arrangement does not take into account widely disjunct geographical ranges, or less obvious anatomical

differences. For example, bone added to the anterior end of the snout of members of the first group is formed by the nasals in *Corythomantis*, the premaxillaries in *Trachycephalus*, and the addition of a prenasal in *Aparasphenodon* and *Triprion*. Furthermore, *Corythomantis* and *Aparasphenodon* have single, median, subgular vocal sacs, *Triprion* a bilobed or single median vocal sac, and *Trachycephalus*, paired lateral vocal sacs. In the second group, *Osteocephalus* has paired, lateral vocal sacs, whereas the others have median, subgular vocal sacs.

It is obvious from the preceding arrangement that the evolution of the casque-headed, so-ossified hylids has resulted in a striking amount of parallelism. Apparently the evolution of species has been largely a process of adaptation to similar environments. However, the wide geographical isolation of seemingly similar genera and the variety of internal and external anatomical characters which separate them in each case cannot be disregarded. Therefore, the casque-headed, co-ossified condition must have arisen at least twice in Middle America (*Triprion* and *Pternohyla*), once in the West Indies (*Hyla septentrionalis* group), and twice in South America (one line composed of *Osteocephalus* and *Trachycephalus* and the other of *Aparasphenodon* and *Corythomantis*).

The development of the casque-headed, co-ossified condition is closely associated with a behavioral trait known as "phragmosis." Barbour (1926) first associated this behavior with frogs which utilize their heads to fill cavities or block holes. Phragmotic behavior has been reported in *Pternohyla*, *Triprion*, *Aparasphenodon*, and *Trachycephalus*. *Pternohyla* is fossorial and thus uses its head to block entries to burrows. *Triprion* blocks tree holes with its head (Stuart, 1935). *Aparasphenodon* plugs entrances to terrestrial bromeliads with its head (Carvalho, 1939), and *Trachycephalus* uses its head to block entrances to both terrestrial bromeliads and tree holes (Lutz, 1950). Phragmotic behavior has not been reported in *Corythomantis greeningi*. The structure of the head in *Corythomantis* and its occurrence in xeric areas where terrestrial bromeliads provide the most likely shelter, suggest that it probably uses its head in the same way that *Aparasphenodon* does. Phragmosis is unknown in *Osteocephalus* and the *Hyla septentrionalis* group. These frogs are inhabitants of more humid, forested areas where suitably moist hiding places are more common.

The development of co-ossification is brought about by the increase of dermal ossification. This structural modification probably

reduces the danger of desiccation in arid environments. The dermal and epidermal layers of skin which overlie membrane bone are poorly organized and characterized by reduced numbers of glands and poor vascularization. Because of the extensive development of bone, the importance of the skin as a sensory and protective organ is diminished. Although it is almost certain that the skin overlying the dorsum of the skull suffers desiccation, the process probably has few, if any, detrimental effects on the physiology of the organism as a whole.

Probably the two most important structural modifications of the skulls with respect to the phragmotic habits of the frogs are the development of labial flanges and extensive dermal roofing bones. In each of the genera exhibiting phragmosis, the roofing bones are fully expanded, or nearly so; thus, there are partial or full articulations between the nasals and partes faciale of the maxillaries, and the paired frontoparietals and nasals are medially convergent. The dermal sphenethmoid has developed from the sphenethmoid; the nasals and frontoparietals articulate with the former in all species except *Pternohyla* and *Tripriion spatulatus*. In these the postero-medial corners of the nasals and the anteromedial corners of the frontoparietals are convergent. The presence of a wide supraorbital shelf, composed of the nasals anteriorly and the frontoparietals posteriorly provides a bony orbital roof under which the frogs can partially or wholly retract their eyes. The auditory region is completely covered by the frontoparietals. This provides protection for the muscles which attach to the anterodorsal surface of the crista parotica and in some cases provides an additional attachment for the *m. rhomboideus anterior* (*occipitosuprascapularis*) which originates on the dorsal parts of the median side of the suprascapula and inserts on the back of the skull. In most of these frogs this muscle is moderately or greatly enlarged, which enables the frogs to flex the head up to nearly a 90-degree angle to the body. Once a frog finds an appropriate shelter, it is capable of fitting its body into a hole or crevice, flexing the head, if necessary, in order to insert its head into the opening, and withdrawing its eyes beneath the bony supra-orbital shelves. A frog thus oriented exposes only its casque head externally, a distinct advantage to the animal in avoiding predators and desiccation.

The development of heavy external ossification in these frogs has been countered with the reduction of bone internally. This is principally a mechanism to reduce the weight of the skull and sec-

ondarily, to reduce the calcium requirements of the frog. The trend towards elimination of bone is especially evident in the cancellous construction of the cranial bones. The palatine is either reduced or absent in the presence of the reinforcement of the maxillary arches anteriorly by the nasals or prenasal, and the medial ramus of the pterygoid is reduced in the presence of a palatine and well developed squamosal.

The development of labial flanges and the associated anterior growth of the maxillaries has resulted in an over-all increase in the length of the skulls of *Aparasphenodon*, *Corythomantis*, and *Triprrion*. The extension of the nasals anterior to the premaxillaries in *Corythomantis* and the addition of the prenasal bone in *Aparasphenodon* and *Triprrion* developed in response to the need of a structural brace at the anterior end of the skull. These bones act as architectural keystones bracing the maxillary arches laterally. The nasals are lengthened anteriorly and provide adequate dorsal coverage for the olfactory region. This anterior extension of bone necessitated the relocation of the external naris anteriorly. The external naris opens directly into the anterolateral part of the cavum principale; thus, once the naris has moved forward, the structure of the olfactory capsule must be reorganized. The posterior part of the olfactory capsule is lengthened and the anterior part moves forward and occupies cavities in the prenasals of *Aparasphenodon* and *Triprrion*, and in the nasals of *Corythomantis*.

Contrary to the other casque-headed, co-ossified hylids, *Pternohyla* is adapted to a fossorial existence. The head is not long; it is depressed and well ossified. *Pternohyla fodiens* has an additional dermal roofing bone on the anterior part of the olfactory capsule. The internasal lies dorsal to the anterior end of the septum nasi between the alary processes. Thus, it does not brace the maxillary arches but probably reinforces the anterior end of the snout. The internal reduction characteristic of the other casque-headed, co-ossified hylids is not evident in *Pternohyla*. The squamosal arch is complete; the palatine robust; and the pterygoid well developed and fully articulated.

## SPECIMENS EXAMINED

The following is an alphabetical list of specimens examined in this study. Only those species which are specifically mentioned in text are included. Unless otherwise designated, the specimens are dry skeletons; "CS" indicates cleared and stained specimens, x-sec., serial cross-sections of the cranium, and x-ray, radiographs of the cranium. Abbreviations for museum specimens are listed below:

AMNH	American Museum of Natural History
CAS	California Academy of Sciences
FMNH	Field Museum of Natural History
KU	University of Kansas Museum of Natural History
LBSC	Long Beach State College
SNM	Senckenbergische Natur-Museum
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum

*Anotheca spinosa*.—KU 59881, 71758, 84899-900.

*Amphignathodon guntheri*.—USNM 163380 (x-ray).

*Aparasphenodon brunoi*.—KU 51326, 92216-18, 92214 (x-sec.).

*Aparasphenodon venezolana*.—SNM 22168 (x-ray).

*Corythomantis greeningi*.—KU 74253, 92222 (x-sec.), 92223-4.

*Gastrotheca ceratophrys*.—KU 104361.

*Gastrotheca marsupiatum*.—KU 99124-7 (CS), 99128-9.

*Gastrotheca nicefori*.—KU 111911 (x-ray).

*Hemiphractus panamensis*.—KU 93504-8.

*Hyla bistrincta*.—KU 69093.

*Hyla boans*.—KU 104402-9.

*Hyla boulengeri*.—KU 41069, 64328 (CS), 84983-4, 87774 (CS), 99191-6, 104350-3, 104846-7.

*Hyla brunnea*.—KU 84693.

*Hyla chaneque*.—KU 58563, 84907-8.

*Hyla dominicensis*.—KU 84701.

*Hyla elaeochroa*.—KU 25207-8, 25221, 41073-84, 68281-91 (CS), 84985-6, 93938 (CS), 104354-6.

*Hyla eximia*.—KU 59902-3 (CS), 92309-10.

*Hyla lancasteri*.—KU 31763, 41087-9, 68298-9, 104325, 104344.

*Hyla lanciformis*.—KU 92507, 99299-301 (CS), 104398-401, 104911 (x-sec.).

*Hyla legleri*.—KU 84987, 87767-8 (CS).

*Hyla microcephala*.—KU 59907-11 (CS), 68293-7 (CS), 68616-22 (CS).

*Hyla miliaria*.—KU 98451.

*Hyla phlebodes*.—KU 41095-8, 68300-07 (CS).

*Hyla rosenbergi*.—KU 41107-08, 68164, 84990-91, 96046-70, 96172-3.

*Hyla rubra*.—KU 74280 (CS), 92151, 104411-2, 111810 (x-sec.).

*Hyla ruficulis*.—KU 41109-112, 68611-12 (CS), 84992, 87765-6 (CS).

*Hyla septentrionalis*.—KU 69098, 72889-98, 84660-1 (CS), 89929-30 (x-sec.), 94151-3; UMMZ S-1309-17, S-1480 (3, CS), S-2452, 106101 (3 of a lot of tadpoles, CS), 108264 (2 of a lot of tadpoles, CS), 108268 (1 of a lot of metamorphosing young, CS).

*Hyla staufferi*.—KU 41113, 59924-7 (CS), 68614-5 (CS).

*Hyla taeniopus*.—KU 55602-3, 59826.

*Hyla uranochroa*.—KU 68165, 68623 (CS), 84993, 87769 (CS).

*Hyla valancifer*.—KU 95416.

*Hyla vasta*.—KU 84711.

SPECIMENS EXAMINED—*Continued*

- Nyctimantis rugiceps*.—KU 109559 (x-ray).  
*Osteocephalus lepieuri*.—KU 99424.  
*Osteocephalus taurinus*.—KU 84725, 92243 (x-sec.), 92247-8.  
*Phrynohyas imitatrix*.—KU 92249.  
*Phrynohyas mesophea*.—KU 92257.  
*Phrynohyas venulosa*.—KU 59880, 68173-7, 111990 (x-sec.); UMMZ S-1184, S-1216.  
*Plectrohyla avia*.—KU 106295.  
*Plectrohyla glandulosa*.—KU 59827-30, 59943-7.  
*Plectrohyla guatemalensis*.—KU 59831-2, 68664.  
*Plectrohyla ixil*.—KU 59833-6.  
*Plectrohyla matudai*.—KU 59948; UMMZ S-1043.  
*Plectrohyla quechii*.—KU 68172.  
*Plectrohyla sagorum*.—UMMZ S-836.  
*Pseudacris triseriata*.—KU 111988 (x-sec.).  
*Pternohyla dentata*.—KU 106291-4, 111989 (x-sec.).  
*Pternohyla fodiens*.—FMNH 98261-8; KU 69145-6 (CS), 86611-15, 89925 (x-sec.).  
*Ptychohyla euthysanota*.—KU 59937-8 (CS).  
*Ptychohyla ignicolor*.—KU 71343 (CS).  
*Ptychohyla leonhardschultzei*.—KU 68630 (CS), 103035 (CS).  
*Ptychohyla schmidtorum*.—KU 59936 (CS), 59940 (CS).  
*Ptychohyla spinipollex*.—KU 59939 (CS), 68631-2 (CS).  
*Smilisca baudini*.—KU 26326-8 (CS), 26332 (CS), 55614 (CS), 55615 (CS), 55616-21, 59801-12, 60024 (1 of a lot of metamorphosing young, CS), 60026 (2 of a lot of metamorphosing young, CS), 60027 (1 of a lot of tadpoles, CS), 62138-9, 68178-84, 69101-3, 84944-9, 89924 (x-sec.).  
*Trachycephalus jordani*.—KU 111994 (x-sec.); LBSC 575 (x-sec.), 577.  
*Trachycephalus nigromaculatus*.—CAS 12659; KU 100353 (x-sec.).  
*Trachycephalus siemersi*.—AMNH 19918 (preserved specimen).  
*Triprion petasatus*.—KU 71473 (x-sec.), 71734 (CS), 71736 (4 of a lot of tadpoles, CS), 71744 (CS), 71759-60, 71778-80, 89926-8 (x-sec.), 92720 (CS); UMMZ S-167.  
*Triprion spatulatus*.—KU 69092, 73845-7, 84901-6, 86925 (x-sec.), 89923 (x-sec.); LBSC 1146; UMMZ S-1769-70, S-1938-9, S-2149, S-2154.

## GLOSSARY

The following is an alphabetical list of technical terms used in the text. Each designation is provided with the abbreviation which has been used for it. The derivations are those given in Webster's Third New International Dictionary. The following abbreviations are used with respect to the derivations: E., English; F., French; Gk., Greek; L., Latin; MF., Middle French; ML., Medieval Latin; NL., New Latin; OF., Old French; S., Spanish.

Acoustic foramen.—*acus. f.*, [Gk. *akoustikos*, of hearing, from *akouein* to hear.] Nerve foramen of the prootic bone in region of the otic capsule. One or two (anterior and posterior) foramina are present, allowing passage of the acoustic nerve (eighth cranial nerve; somatic sensory) from the floor of the medulla to the cristae and maculae of the internal ear.

Alary cartilage.—*al. c.*, [L. *alarius* from *ala*, wing + *-arius*, -ary.] A principal cartilage of the olfactory capsule. The cartilage surrounds the anterolateral aspect of the *cavum principale* anterior to the external naris; it is fused with the superior prenasal cartilage anteriorly, and usually with the *solum nasi* posteromedially.

Alary process.—*al. proc.*, [L. *alarius* from *ala*, wing + *-arius*, -ary.] Dorsomedial bony process of the premaxillary bone of the upper jaw. Process serves as an anterior abutment for the superior and inferior prenasal cartilages of the olfactory capsule.

Angulosplenic.—*angsp.*, [L. *angulo* from *angulus*, angle + *splenic* from *splenium*, patch.] Dermal bone of the lower jaw. The bone lies medial and posteriorly, ventrally adjacent to Meckel's cartilage.

Anterior acoustic foramen.—*ant. acus. f.*, see acoustic foramen.

Anterior arm of the squamosal.—That part of the squamosal which extends anteroventrally from the crista parotica towards the maxillary, thereby forming a partial or complete posterior margin to the orbit.

Anterior maxillary process.—*ant. max. proc.* Small rod of cartilage which lies medially adjacent to the maxillary anterior to the planum antorbitale. The process terminates at the planum antorbitale.

Anterior ramus of the pterygoid.—That branch of the pterygoid which lies medially adjacent to the maxillary and posterior maxillary process. The anterior end of the ramus usually lies between the levels of the orbitonasal foramen, anteriorly, and the mid-orbital region, posteriorly.

Bursa angularis oris.—*b. ang. o.*, [ML. *bursa*, bag; L. *angulus*, angle; L. *ora*, border or edge.] Tubular lymphoid gland which lies between the maxillary laterally, and the pterygoid process and pterygoid, medially, in the posterior part of the orbit. Function of the gland is unknown.

Canthal ridge.—[Gk. *kanthos*, angle.] Dorsal angle of the nasal. Ridge may be sharp or indistinct and usually extends from the orbit, posteriorly, to the tip of the snout, anteriorly.

Cartilage.—*c.*, [L. *cartilago*, akin to L. *cratis*, wickerwork.] A specialized, fibrous connective tissue which forms the chondocranium of adult and larval anurans and gives rise to endochondral bones of the osteocranium of the adult.

Cartilaginous sclera.—*c. scl.*, [NL. from Gk. *skleros*, hard.] The internal, cartilaginous tunic of the eyeball.

Cartilago obliquo.—*c. obl.*, [L. *obliquus*, slanting.] Nasal capsule cartilage which diverges posterolaterally from the dorsal tectum nasi to join the lamina inferior laterally and thereby form the planum terminale.

Casque.—[influenced by F. *casque* from S. *casco*, potsherd, skull, helmet, cask.] The expansion and thickening of dermal roofing bones and jaw bones.

Cavum.—*cav.*, [L. *cava* from *cavus*, hollow.] A cavity.

- Cavum inferius.**—*cav. inf.* The most ventral of the three nasal cavities contained in the nasal capsule.
- Cavum medium.**—*cav. med.* The smallest of the three nasal cavities. This cavity lies between the cavum inferius and principale. Posteriorly the nasolacrimal duct diverges laterally from the cavum medium.
- Cavum principale.**—*cav. prin.* The largest and most dorsal of the three nasal cavities contained in the nasal capsule. The external naris opens into the anterolateral part of the cavum principale.
- Columella.**—*col.*, [NL. from L., small column, diminutive of *columna*, columnn.] The cartilaginous and bony rod which connects the tympanum with the inner ear in amphibians; the stapes.
- Co-ossification.**—[*co-*, from L. *com-* with + ossification, probably from NL. *ossificatus* (past participle of *ossificare*, to ossify) + L. *-ion*, *-io*, *-ion*.] The formation of bone, continuous with the underlying dermal bone, in the dense connective tissue dermis of the skin.
- Cornu principalis.**—*corn. prin.*, [L. *cornu*, horn.] The terminal portion of the posterolateral process of the hyale, which joins the hyoid apparatus to the pseudobasal process of the osteocranium.
- Crista.**—*cr.*, [L. *crista*, crest.]
- Crista intermedia.**—*cr. int.* A bridge of cartilage uniting the lamina inferior and lamina superior, laterally, with the septum nasi, medially, in the anterior part of the olfactory capsule.
- Crista parotica.**—*cr. par.*, [NL. *paroticus* from L. *para-*, *para-* + NL. *oticus*, otic, from Gk. *otikos*, relating to the ear.] The dorsal part of the prootic which overlies the columella and extends from the braincase, medially, to the squamosal, laterally.
- Crista subnasalis.**—*cr. sub.*, [NL. from *sub-*, under + *nasalis*, nasal.] A small rod of cartilage which diverges posterolaterally from the solum nasi ventral to the anterior end of the nasal capsule, and lies adjacent to the maxillary.
- Dentary.**—*den.*, [L. *dentalis*, from *dent-*, *dens*, tooth + E. *-ary*.] Dermal bone of the lower jaw of anurans. Bone is located anterolateral to Meckel's cartilage and articulates anteriorly with the mentomeckelian.
- Dermal sphenethmoid.**—*derm. spheth.*, [NL. from Gk. *derm-*, dermo-, from *derein*, to skin; NL. from Gk. *sphen-*, wedge + *ethmoeides*, like a strainer.] The dorsal, dermal component of the endochondral sphenethmoid. The bone is co-ossified with the overlying skin, completely fused with the underlying bone, and usually articulates with the nasals anteriorly and frontoparietals posteriorly.
- Duct.**—*dt.*, [L. *ductus*, act of leading, shape.]
- Eminence.**—*em.*, [L. *eminentia*, prominence.]
- Endochondral sphenethmoid.**—*spheth.*, [Gk. *endon*, within + *chondros*, cartilage; NL. from Gk. *sphen-*, wedge + *ethmoeides*, like a strainer.] The large, endochondral bone forming the anterior end of the braincase. The sphenethmoid lies between the olfactory capsules anteriorly and the prootic posteriorly.
- Epiotic eminence.**—*epi. em.*, [Gk. *epi-*, on, upon, to + *-otic*, of the ear.] Dorsal part of otic capsule which lies medial to crista parotica.
- Eustachian tube.**—*E. t.* [Eustacian, in reference to Bartolommeo Eustachio, an Italian anatomist, 1520-1574.] Tube connecting tympanic cavity with pharynx.
- Exoccipital.**—*exocc.*, [Gk. *exo-*, out of, outside of + ML. *occipitalis*, from L. *occipit*, *occiput* + *-alis*, *-al*, back formation.] An endochondral bone forming the posterior end of the braincase, posterior to the prootic and around the foramen magnum. The exoccipital is usually fused with the prootic in adult anurans.
- External naris.**—*ext. nar.*, [L. akin to L. *nasus*, nose.] The nostril or the opening of the cavum principale of the olfactory capsule to the exterior.

Fontanelle.—*fon.*, [ME. *fontinelle*, from MF. *fontenele*, little spring, diminutive of *fontaine*, spring.] A gap(s) in cranial roofing bones.

Foramen.—*f.*, [L. from *forare*, to bore, pierce.] The aperture or opening through a bone or membrane for the passage of blood vessels and/or nerves.

Frontoparietal.—*fpar.*, [L. *frons*, forehead + *parietal*, MF. from NL. *pariet-*, *paries*, wall + MF. -*al*.] Paired dermal roofing bones which overlie the sphenethmoid and prootic in anurans.

Frontoparietal fontanelle.—*fpar. fon.* A gap in the endochondral cranial roof of anurans formed in the sphenethmoid anteriorly and the prootic posteriorly. The fontanelle is covered by membranous connective tissue. In addition, it may be covered partially or completely by the frontoparietals dorsally.

Inferior prenasal cartilage.—*inf. pnas. c.* Anterior and ventral nasal capsule cartilage which extends from floor of olfactory capsule anterior to the base of the alary process of the premaxillary.

Infundibulum.—*inf.*, [NL. from L., funnel, from *infundere*, to pour in.] Any funnel-shaped anatomical structure. Refers here to pocket formed at posterior end of *cavum medium*.

Intermedia.—*intm.*, [NL. from L., feminine of *intermedius*, intermediate.]

Internal naris.—*int. nar.*, [L. akin to L. *nasus*, nose.] The choana or the opening of the *cavum principale* and *cavum inferius* into the oral cavity.

Internasal.—[L. *inter*, between + L. *nasus*, nose + -*alis*, -*al*.] Dermal roofing bone which lies anterior to nasals and between external nares.

Jugular foramen.—*jug. f.*, [L. *jugulum*, collarbone, neck, throat akin to L. *jungere*, to join.] Nerve foramen of the prootic and exoccipital. Foramen lies just posterior to the otic capsule and allows passage of glossopharyngeal (ninth cranial nerve; visceral sensory and motor) and vagus (tenth cranial nerve; visceral sensory and motor) nerves from medulla.

Lamina.—*lam.*, [L. *lamina*, a thin plate.]

Lamina inferior.—*lam. inf.* A thin plate of cartilage which lies between the *cavum medium* and *cavum inferius* of the olfactory capsule. Anteriorly lamina differentiates from *solum nasi*; posteriorly, the lateral part of the lamina fuses with the *cartilago obliqua* to form the *planum terminale*.

Lamina perpendicularis.—*lam. perp.*, [from L. *perpendicularis*, from *perpendicularum*, plumb line (from *per-*, through + *pendere*, to hang + -*iculum*, suffix denoting an instrument).] Bony ventral flange of the frontoparietal which forms the dorsolateral corner of the braincase in the region of the synchondrotic union of the sphenethmoid and prootic.

Lamina superior.—*lam. sup.* A thin plate of cartilage which lies between the *cavum principale* and *cavum medium* of the olfactory capsule. Anteriorly, the lamina differentiates from the *solum nasi*; posteriorly, the lamina is associated with the medial ramus of the septomaxillary.

Lateral process of parasphenoid.—The basal wing, or that, posterior part of the parasphenoid which invests the otic capsule ventrally.

Marginalis.—*mar.*, [L. *margo*, border + -*alis*, -*al*.]

Maxillary.—*max.*, [L. *maxilla*, jaw, diminutive of *mala*, jawbone.] The principal bone of the upper jaw. Maxillary articulates with the premaxillary anteriorly, and usually the quadratojugal posteriorly.

Meckel's cartilage.—*Mc. c.*, [Meckel's in reference to Johann Friedrich Meckel, Junior, a German anatomist (died 1833).] The cartilaginous rod of the lower jaw which lies medial to the dentary anteriorly, and lateral and dorsal to the angulosplenic posteriorly. Meckel's cartilage articulates with the cartilaginous quadrate process in the articular region.

Medial.—[L. *medius*, middle.]

Medial ramus of the pterygoid.—*med. r. pter.* That branch of the pterygoid which extends toward, and sometimes articulates with, the anteroventral corner of the otic capsule.

- Mentomeckelian.**—*mmk.*, [combination form, from *L. mentum*, chin + *meckel*, in reference to Johann Friedrich Meckel, Junior, a German anatomist + *-ian*.] A small endochondral bone of the lower jaw. The bone is located lateral to the mandibular symphysis and articulates laterally with the dentary.
- Nasal.**—*nas.*, [from *L. nasale*, neuter singular of *nasalis*, nasal, from *L. nasus*, nose + *-alis*, *-al*.] Paired dermal roofing bones which cover the olfactory capsule anterior to the sphenethmoid.
- Nasal process.**—*nas. proc.* A posterolateral process of the nasal which extends towards and articulates with the pars facialis of the maxillary in some species.
- Nasolacrimal duct.**—*nlc. dt.*, [combination form, from *L. nasus* + *L. lacrima*, tear + *-alis*, *-al*.] The tear duct extending from the posterolateral corner of the cavum medium to the orbit.
- Occipital crest.**—[*ML. occipitalis*, from *L. occipit*, *occiput* + *-alis*, *-al*, back formation.] Transverse crest sometimes present at the posterior edge of the frontoparietal.
- Oculomotor foramen.**—*ocul. f.*, [combination form, from *L. ocul-* from *oculus*, eye + *L. motus* (past participle of *movere*) to move + *-or*.] Small foramen located posterior to the optic foramen in the prootic bone. Foramen allows passage of third cranial nerve (somatic motor) from midbrain to inferior oblique, superior, inferior, and internal recti, and some accessory muscles of the eyeball.
- Odontoid.**—[*Gk. odontoeides*, from *odont-*, tooth + *-oeides* form, *-oid*.] A structure which is tooth-like in appearance.
- Olfactory capsule.**—[*L. olfactorius*, from *olfactus*, *olefactus* (past participle of *olfacere*, *olefacere* from *olere*, to smell + *facere*, to make, do) + *-orius*, *-ory*.] The olfactory bulb, or the entire complex of nasal structures including the nasal cavities and associated cartilages.
- Olfactory eminence.**—*olf. em.* A protuberance from the floor of the posterior part of the olfactory capsule. Structurally the olfactory eminence involves the epithelium of the nasal cavity, the cartilaginous support of the solum nasi, and the bony support of a dorsal process of the prevomer.
- Operculum.**—*Op.*, [*NL.* from *L.* cover, lid, from *operire*, to cover, shut (from *op-*, *ob* to, before + (assumed) *-verire*, to shut) + *-culum*, suffix denoting an instrument).] A plate-like structure which articulates with the pars interna plectri of the columella or stapes and covers the oval window of the internal ear.
- Optic foramen.**—*opt. f.*, [*MF. optique* from *ML. opticus* from *Gk. optikos* from *optos* + *-ikos*, *-ic*.] Large foramen located in cartilage between sphenethmoid and prootic bones. Foramen allows passage of the optic tract of the brain from the diencephalon to the retina.
- Orbit.**—*orb.*, [*L. orbita*, circuit.] Cavity, surrounded by cranial bones, in which the eye is located.
- Orbitonasal foramen.**—*orbnas. f.*, [combination form, from *L. orbita*, circuit + *L. nasus*, nose.] Conspicuous bony foramen which is located in the sphenethmoid in the anterior end of the orbit, and allows passage of blood vessels and nerves from orbit to snout.
- Otic capsule.**—*ot. cap.*, [*NL. oticus*, from *Gk. otikos*, relating to the ear.] That part of the prootic lateral to the braincase, which houses the internal ear consisting of the membranous labyrinth.
- Otic process.**—*ot. proc.*, [*NL. oticus*, from *Gk. otikos*, relating to the ear.] A cartilaginous process uniting the anterolateral corner of the crista parotica to the pseudobasal process.
- Palatine.**—*pal.*, [*F. palatin*, from (assumed) *NL. palatinus*, from *L. palatum*, palate + *-inus*, *-ine*.] Paired dermal bone of support located at anterior end of orbit. Distally, the palatine articulates with the maxillary; medially, the bone usually articulates with the sphenethmoid.

- Palatine process.—*pal. proc.*, [L. *palatum*, palate + *-inus*, *-ine*.] Small, pointed process located posteromedially on pars palatina of premaxillary.
- Parasphenoid.—*psrph.*, [para-, from L., from Gk. *para* (akin to Gk. *pro*, before, ahead) + sphenoid from Gk. *sphen*, wedge + *-oeides*, *-oid*.] Dermal investing bone which is located ventral to the posterior part of the sphenethmoid and the prootic.
- Pars.—*p.*, [L., one that is equal, from *par*, equal.]
- Pars ascendens plectri.—*p. asc. pl.* A small rod of cartilage which extends from the distal part of the columella, the pars externa plectri, to the distal end of the crista parotica dorsally.
- Pars dentalis.—*p. dent.*, [L. *dentatus*, from *dent-*, *dens*, tooth + *-alis*, *-al*.] The tooth-bearing parts of the maxillary and premaxillary.
- Pars externa plectri.—*p. ext. pl.* The distal cartilaginous part of the columella which lies adjacent to the tympanic membrane.
- Pars facialis.—*p. fac.*, [ML. *facialis*, from L. *facies*, form, shape + *-alis*, *-al*.] Dorsomedially inclined flange of bone arising from ventral, longitudinal axis of the maxillary.
- Pars interna plectri.—*p. int. pl.* Proximal, cartilaginous segment of the columella which lies adjacent to the otic capsule and articulates with the operculum posteriorly.
- Pars media plectri.—*p. med. pl.* Medial, ossified part of the columella which lies between the pars interna plectri, medially, and the pars externa plectri, laterally.
- Pars palatina.—*p. pal.* Lingual flange of bone dorsal to pars dentalis of maxillary and premaxillary bones.
- Planum.—*pla.*, [L. *planum*, level surface.]
- Planum antorbitale.—*pla. ant.*, [ant-, ME. from L. *ante*, before, in front of + orbit, L. *orbita*, circuit + *-al*, of, or relating to.] Posterolateral part of the olfactory capsule lying in synchondrotic continuity with the sphenethmoid posteriorly.
- Planum terminale.—*pla. term.*, [L. *termino*, limit, level, end + *-al*, of, or relating to.] Cartilage surrounding lateral part of olfactory capsule posterior to external naris. Planum terminale formed by fusion of lamina inferior and cartilago obliquus.
- Plectri.—*pl.*, [L. from Gk. *plektron*, striking instrument.]
- Posterior acoustic foramen.—*post. acus. f.* See acoustic foramen.
- Posterior arm of squamosal.—That part of the squamosal which extends posteriorly from union of anterior and ventral arms of the squamosal. Posterior arm usually articulates with crista parotica.
- Posterior maxillary process.—*post. max. proc.* Small rod of cartilage which lies medially adjacent to the maxillary between the levels of the planum antorbitale anteriorly and the divergence of the pterygoid and pterygoid process from the maxillary posteriorly.
- Posterior ramus of pterygoid.—That branch of the pterygoid which articulates posteriorly with the quadrate process of the articular region.
- Premaxillary.—*pmax.*, [pre-, ME. from OF. and L. *prae*, before + maxillary from L. *maxilla*, jaw.] Anterior, dermal bone of the upper jaw. Premaxillary bears a dorsal alary process and articulates with the maxillary laterally.
- Prenasal.—*pnas.*, [pre-, ME. from OF. and L. *prae*, before + nasal from L. *nasus*, nose + *-alis*, *-al*.] Dermal bone which lies anterior to premaxillaries, maxillaries, and nasals, and forms the anterior end of the snout.
- Preorbital knob.—*porb. kb.*, [pre-, ME. from OF. and L. *prae*, before + L. *orbita*, circuit + *-al*, of, or relating to.] Nasal prominence formed at the posterior end of the canthal ridge at the edge of the orbit.

- Prevomer.**—*pvom.*, [pre-, ME. from OF. and L. *prae*, before + L. *vomis*, vomer, plowshare.] Paired dermal investing bones located ventral to the solum nasi of the olfactory capsule. Prevomer bears a dorsal process which provides internal support for the olfactory eminence, and usually a posterior dentigerous process.
- Principale.**—*prin.*, [from L. *principalis*, first, principal.]
- Process.**—*proc.*, [from L. *processus* (past participle of *procedere*, to procede).]
- Prootic.**—*pro.*, [pro-, L. from *pro*, before, in front of + otic, from NL. *oticus* from Gk. *otikos*, relating to the ear.] Endochondral bone which forms otic capsules and braincase posterior to the sphenethmoid.
- Prootic foramen.**—*pro. f.* Large foramen located posterior to oculomotor foramen in prootic bone. This foramen allows the passage of three cranial nerves and their branches from the floor and side of the medulla to various parts of the head. The cranial nerves included are as follow: (1) trigeminal (fifth cranial nerve; mixed somatic and visceral sensory) with three branches, the ophthalmic (to orbit and nasal region), maxillary (to upper jaw and roof of oral and pharyngeal cavities), and mandibular (to lower jaw and floor of oral and pharyngeal cavities); (2) abducens (sixth cranial nerve; somatic motor) to external rectus muscle of eyeball; and (3) facial (seventh cranial nerve; sensory and visceral motor) to taste buds, pharyngeal lining and muscles of hyoid arch.
- Pterygoid.**—*pter.*, [probably from (assumed) NL. *pterygoides* from Gk. *pterygoeides*, winglike.] Paired, triradiate dermal bones of support located in posterolateral part of skull between articular region, otic capsule, and orbit.
- Pterygoid process.**—*pter. proc.* Cartilaginous process associated with the pterygoid and continuous with the posterior maxillary process anteriorly and the quadrate process posteriorly.
- Quadrate process.**—*quad. proc.*, [from L. *quadratum*, from neuter of *quadratus*, square]. Cartilaginous process of the articular region. Quadrate process is continuous with the pterygoid process anteriorly. Posteriorly, it articulates with the quadratojugal, ventral arm of the squamosal, posterior ramus of the pterygoid and Meckel's cartilage.
- Quadratojugal.**—*qi.*, [quadrat-, from L. *quadratus*, square + -o- + -jugal, from L. *jugalis*, from *jugum*, yoke.] Small, dermal bone of upper jaw. Quadratojugal articulates with maxillary anteromedially; posteriorly ossification of the quadratojugal invades cartilage of the quadrate process. The bone is often reduced or lost.
- Ramus.**—*r.*, [from L. *ramus*, branch.]
- Septomaxillary.**—*spmax.*, [sept-, from L. *septum*, partition + -o- + maxillary, from L. *maxilla*, jaw.] Small bone which is internal to olfactory capsule and of uncertain (endochondral or dermal) origin. Septomaxillary is located around cavum medium. A ventral ramus or loop supports the divergence of the nasolacrimal duct from the cavum, whereas dorsal, lateral, and medial rami support the union of the cavum principale and cavum inferius through the posterior end of the cavum medium.
- Septum.**—*sept.*, [L. *septum*, partition.]
- Septum nasi.**—*sept. nas.* Cartilaginous partition between the olfactory capsules. Septum is synchondrotically united with sphenethmoid posteriorly.
- Solum.**—*sol.*, [L. *solum*, floor.]
- Solum nasi.**—*sol. nas.* Cartilaginous floor of olfactory capsules. Ossification is usually present in posterior parts of solum.
- Sphenethmoid.**—*spheth.*, [Gk. *sphen-*, wedge + *ethmoeides*, like a strainer.] Endochondral bone forming anterior end of braincase between olfactory capsules, anteriorly, and prootic, posteriorly.
- Squamosal.**—*sq.*, [L. *squamosus*, squamous + E. -al, scale-like.] Paired, tri-radiate dermal bones located at posterolateral corners of skull. Anterior and posterior arms usually articulate with the crista parotica of the prootic; the ventral arm articulates with the quadrate process of the upper jaw.

Superior prenasal cartilage.—*sup. pnas. c.* Anterior and dorsal nasal capsule cartilage which extends from alary cartilage anterior to the dorsal part of the alary processes of the premaxillary.

Synchondrotic.—adjective from synchondrosis, [Gk. *syn*, with + *chondros*, cartilage.] The union of two or more separate cranial elements by cartilage.

Synosteotic.—also synostotic; adjective from synosteosis or synostosis, [Gk. *syn*, with + *osteon*, bone.] Ossification from two or more centers in the same bone.

Taenia.—*t.*, [L., head, band.]

Taenia tecta marginalis.—*t. t. mar.* Cartilage of the sphenethmoid bordering the frontoparietal fontanelle.

Tectum.—*tect.*, [L., roof.]

Tectum nasi.—*tect. nas.* Cartilaginous roof of the nasal capsule. Tectum nasi is continuous with the septum nasi and gives rise to the cartilago obliquus posterolaterally.

Tectum synoticum.—*tect. syn.*, [syn-, Gk. *syn*, with, together with + *otikos*, relating to the ear.] Cartilaginous roof of the prootic which unites the otic capsules.

Trochlear foramen.—*troc. f.*, [NL. *trochlearis*, from *trochlea* + L. *-aris*, -ar, sheath of pulleys, from Gk. *trochileia* (akin to Gk. *trochos*, wheel).] Small nerve foramen for fourth cranial nerve (somatic motor). Foramen located dorsal or posterodorsal to optic foramen; it lies within bony margins of optic foramen or in the lamina perpendicularis of the frontoparietal. Allows passage of trochlear nerve from midbrain to inferior oblique, superior, inferior and internal recti, and some accessory muscles of the eyeball.

Tympanic ring.—*tymp. r.*, [L. and NL. *tympanum*, drum + E. *-ic*, from Gk. *tympanon*, drum (akin to Gk. *typtein*, to strike, beat).] Ring of cartilage surrounding tympanic membrane of ear.

Ventral arm of the squamosal.—*sq.* That part of the squamosal which extends posteroventrally from the union of the anterior and posterior arms of the squamosal, dorsally, to the articular region, ventrally.

## LITERATURE CITED

- BALDAUF, R. J.  
1955. Contributions to the cranial morphology of *Bufo w. woodhousei* Girard. Texas J. Sci., 7:275-311.  
1957. Additional studies on the cranial morphology of *Bufo w. woodhousei* Girard. Texas J. Sci., 9:84-88.  
1958a. Contributions to the cranial morphology of *Bufo valliceps* Wiegmann. Texas J. Sci., 10:172-186.  
1958b. A procedure for the staining and sectioning of the heads of adult anurans. Texas J. Sci., 10:448-451.
- BALDAUF, R. J., and E. C. TANZER  
1965. Contributions to the cranial morphology of the leptodactylid frog, *Syrhophus marnocki* Cope. Texas J. Sci., 17:71-100.
- BARBOUR, T.  
1926. Reptiles and amphibians. Their habits and adaptations. Houghton-Mifflin Co., New York, New York. xx + 125 pp.
- BOKERMANN, W. C. A.  
1964. Field observations on the hylid frog *Osteocephalus taurinus* Fitz. Herpetologica, 20:252-255.  
1966. Una nueva especie de *Trachycephalus* da Bahia, Brasil. Neotropica, 12:120-124.
- BOULENGER, G. A.  
1882. Description of a new genus and species of frogs of the family Hylidae. Ann. Mag. Nat. Hist., ser. 5, 10:326-328.  
1896. Descriptions of new batrachians in the British Museum. Ann. Mag. Nat. Hist., ser. 6, 17:401-406, pl. 17.
- CARVALHO, A. L. DE  
1939. Nota previa sobre os habitos de uma interessante "perereca" bromelicola do litoral SE Brasileiro. O Campo, Rio de Janeiro, Brazil, pp. 25-26.  
1941. Notas sobre os generos *Corythomantis* Boulenger e *Aparasphenodon* Miranda Ribeiro; Amphibia-Anura-Hylidae. Papéis Avulsos Dept. Zool., São Paulo, 1:101-110.
- COCHRAN, D. M.  
1955. Frogs of southeastern Brazil. Bull. U. S. Natl. Mus., 206:xvi + 409 pp., pls. 1-34.
- COCHRAN, D. M., and C. J. GOIN  
1968. The frogs of Colombia. Bull. U. S. Natl. Mus. (in press).
- COPE, E. D.  
1865. Third contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 17:185-198.  
1866. Fourth contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 18:123-132.  
1874. On some Batrachia and Nematognathi brought from the Upper Amazon by Professor Orton. Proc. Acad. Nat. Sci. Philadelphia, 26:120-132.  
1877. Catalogue of batrachians and reptiles of Central America and Mexico. Bull. U. S. Natl. Mus., 32:1-98.
- DARLINGTON, P. J.  
1957. Zoogeography: the geographical distribution of animals. John Wiley and Sons, Inc., New York, xi + 675 pp.

- DE BEER, G. R.  
1937. The development of the vertebrate skull. Oxford. xxiii + 552 pp., pls. 1-143.
- DUCKE, A., and G. A. BLACK  
1953. Phytogeographical notes on the Brazilian Amazon. Ann. Acad. Brasileira Cien., 25:1-46.
- DUELLMAN, W. E.  
1956. The frogs of the hylid genus *Phrynohyas* Fitzinger, 1843. Misc. Publ. Mus. Zool., Univ. Michigan, 96:1-47, pls. 1-6.  
1958. A monographic study of the colubrid snake genus *Leptodeira*. Bull. Amer. Mus. Nat. Hist., 114:1-152, pls. 1-31.  
1960. A distributional study of the amphibians of the Isthmus of Tehuantepec, Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 13:19-72, pls. 1-8.  
1968. The taxonomic status of some American hylid frogs. Herpetologica, 24:194-209.
- DUELLMAN, W. E., and L. T. KLAAS  
1964. The biology of the hylid frog *Triprrion petasatus*. Copeia, 1964: 308-321.
- DUELLMAN, W. E., and A. SCHWARTZ  
1958. Amphibians and reptiles of southern Florida. Bull. Florida State Mus., 3:181-324.
- DUELLMAN, W. E., and L. TRUEB  
1966. Neotropical frogs of the genus *Smilisca*. Univ. Kansas Publ., Mus. Nat. Hist., 17:281-375, pls. 1-12.
- DUMÉRIL, A. M. C., and G. BIBRON  
1841. *Erpétologie générale ou histoire naturelle complete des reptiles*. Paris, vol. 8:iv + 792 pp.
- DUNN, E. R.  
1926. The frogs of Jamaica. Proc. Boston Soc. Nat. Hist., 38:111-130, pls. 1-2.
- ERDMANN, K.  
1933. Zur Entwicklung des knöchernen Skelets von *Triton* und *Rana* unter besonderer Berücksichtigung der Zeitfolge der Ossifikationen. Z. Anat. EntwGes., 101:566-651.
- FITZINGER, L. J.  
1843. *Systema reptilium*. Vienna, vi + 106 pp.  
1864. *Bilder-atlas zur Wissenschaftlich-populären Naturgeschichte der Amphibien*. Vienna, 109 pls.
- GOIN, C. J.  
1961. Synopsis of the genera of hylid frogs. Ann. Carnegie Mus., 36:5-18.
- GOSNER, K. L.  
1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica, 16:183-190.
- GÜNTHER, A. C. L. G.  
1882. Notice of a second species of *Triprrion*. Ann. Mag. Nat. Hist., ser. 5, 10:279.
- KELLOGG, R.  
1932. Mexican tailless amphibians in the United States National Museum. Bull. U. S. Natl. Mus., 160:iv + 224 pp.

- KING, W.  
1962. The occurrence of rafts for dispersal of land animals into the West Indies. *Quart. Jour. Florida Acad. Sci.*, 25:45-52.
- LEON, JUAN R.  
1969. The systematics of the frogs of the *Hyla rubra* group in Middle America. *Univ. Kansas Publ., Mus. Nat. Hist.*, 18(6):505-545.
- LUTZ, A.  
1926. New species of Brazilian batrachians. Preliminary note. (Trabalho do Instituto Oswaldo Cruz.) Published by author at Manguinhos, 16 pp.
- LUTZ, B.  
1954. Anfíbios Anuros do Distrito Federal. *Mem. Inst. Oswaldo Cruz*, 52:155-238.
- LUTZ, B., AND G. R. KLOSS  
1952. Short notes on some frogs from the upper Amazons and a few vicariant forms. *Mem. Inst. Oswaldo Cruz*, 50:629-678.
- LYNN, W. G.  
1942. The embryology of *Eleutherodactylus nubicola*, an anuran which has no tadpole stage. *Contributions to embryology. Carnegie Inst. Washington Publ.* 541, 30:27-62.
- MERTENS, R.  
1937. Ein neuer Laubfrosch aus Argentinien. *Senckenbergiana*, 19:12-14.  
1939. Herpetologische Ergebnisse einer Reise nach der Insel Hispaniola, Westindien. *Abhandl. Senckenberg. Naturforsch. Gesellsch.*, 449:84 pp., 10 pls.  
1950. Ein neuer Laubfrosch aus Venezuela. *Senckenbergiana*, 31:1-2.
- MIRANDA-RIBEIRO, A. DE  
1920. *Triprion, Diaglena, Corythomantis*, etc. uma subseccao de Hylidae, com duas especies novas. *Rev. Mus. Paulista*, 12:83-88, 2 pls.  
1937. Sobre uma colleccão de vertebrados do nordeste brasileiro. *O Campo*, 1937 (Jan):54-56.
- MOCQUARD, M. F.  
1899. Reptiles et batraciens recueillis au Mexique par M. León Diguët en 1896 et 1897. *Bull. Soc. Philom. Paris, Ser. 9*, 1:154-169, pl. 1.
- MYERS, G. S.  
1942. Notes on some frogs from Peru and Ecuador. *Proc. Biol. Soc. Washington*, 55:151-156.  
1950. The systematic status of *Hyla septentrionalis*, the large tree frog of the Florida Keys, the Bahamas, and Cuba. *Copeia*, 1950:203-214.
- NOBLE, G. K.  
1923. Field studies of Dominican tree frogs and their haunts. *Nat. Hist.*, 22:117-121.
- OLIVEIRA, A. I. DE  
1956. Brazil. In Jenks, W. F. (ed.). *Handbook of South American geology. Mem. Geol. Soc. Amer.*, 65:3-62.
- PETERS, J. A.  
1955. Notes on the frog genus *Diaglena* Cope. *Nat. Hist. Misc., Chicago Acad. Sci.*, 143:1-8.
- RIVERO, J. A.  
1961. Salientia of Venezuela. *Bull. Mus. Comp. Zool., Harvard College*, 126:1-207.

SAVAGE, D. E.

1955. A survey of various late Cenozoic vertebrate faunas of the panhandle of Texas. Pt. II. Univ. California Publ. Geol. Sci., 31:51-74, pls. 1-2.

SAVAGE, J. M.

1966. The origins and history of the Central American herpetofauna. Copeia, 1966:719-766.

SIMPSON, G. G.

1956. Zoogeography of West Indian land mammals. American Mus. Novitates, 1759:1-28.

SMITH, C. L., and G. R. SMITH

1967. A technique for making stereoscopic radiographs of animal skeletons. Copeia, 1967:848-850.

SMITH, H. M.

1957. A new casque-headed frog (*Pternohyla*) from Mexico. Herpetologica, 13:1-4.

STEINDACHNER, F.

1862. Über zwei noch unbeschriebene Batrachier aus den Sammlungen des K. K. zoologischen Museums. Arch. Zool. Anat. Fis., 1862:77-82.  
1864. Batrachologische Mitteilungen. Verh. Zool. Bot. Ges. Wein, 14 (1-2):239-288, pls. 9-17.

STEJNEGER, L., and F. C. TEST

1891. Description of a new genus and species of tailless batrachian from tropical America. Proc. U. S. Natl. Mus., 14:167-168, pl. 3.

STOKELY, P. S., and J. C. LIST

1954. The progress of ossification in the skull of the cricketfrog *Pseudacris nigrata triseriata*. Copeia, 1954:211-217.

STUART, L. C.

1935. A contribution to a knowledge of the herpetology of a portion of the savanna region of central Petén, Guatemala. Misc. Publ., Mus. Zool. Univ. Michigan, 29:1-56.

TAYLOR, E. H.

1942. The frog genus *Diaglena* with a description of a new species. Univ. Kansas Sci. Bull., 28:57-65.

TRUEB, L.

1966. Morphology and development of the skull in the frog *Hyla septentrionalis*. Copeia, 1966:562-573.  
1968. Internal cranial anatomy of the hylid frog *Smilisca baudini*. Univ. Kansas Publ., Mus. Nat. Hist., 18(2):11-35.

TSCHUDI, J. J.

1838. Classification der Batrachier mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien. Neuchatel, 102 pp., 6 pls.

VELOSO, H. P.

1947. Considerações gerais sobre a vegetação do Estado de Mato Grosso I —Notas preliminares sobre o cerrado. Mem. Inst. Oswaldo Cruz, 44:579-603, figs. 1-19.

WERNER, F.

1893. Herpetologische Nova. Zool. Anz., 13:81-84.